JBM 1010

Bulletin British Museum (Natural History)

Botany Series

VOLUME 20 NUMBER 2 20 DECEMBER 1990

SHOUT
SHARE
IT

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

The Botany Series is edited in the Museum's Department of Botany

Keeper of Botany:	Dr S. Blackmore
Editor of Bulletin:	Dr R. Huxley
Assistant Editor:	Dr A. J. Harrington
Assistant Editor:	Mrs M. J. West

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 256 pages, made up of two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Sales Department,
Natural History Museum Publications,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

Telephone: 071-938-9386
Telex: 929437 NH PUBS G
Fax: 071-938-8709

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Bot.)

© British Museum (Natural History), 1990

ISBN 0 565 08027 X
ISSN 0068 – 2292

Botany Series
Vol **20**(2), pp 153 – 237

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 20 December 1990

Typeset by J & L Composition, Filey, N. Yorks.
Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Bull. Br. Mus. nat. Hist (Bot.) **20**(2): 153–168 Issued 20 December 1990

BRITISH MUSEUM
(NATURAL HISTORY)
14 JA
PRESENTED
GENERAL LIBRARY

The marine algal flora of Namibia: its distribution and affinities

GEORGE W. LAWSON
23 Sheffield Terrace, London W8 7NQ
RICHARD H. SIMONS
Department of Botany, University of Cape Town, Rondebosch, South Africa 7700
WILLIAM EDWIN ISAAC
20 Spraypoint Road, Blairgowrie, Victoria 3942, Australia

BM 91455

CONTENTS

Introduction 153
The Namibian coast and its environmental conditions 154
Patterns of littoral zonation 154
The phytogeographical status of the Namibian marine algal flora 161
Annotated list of species 164
References 167

Synopsis. The coast of Namibia (South West Africa) which lies partly within and partly outside the tropics on the south western Atlantic coast of Africa was visited and studied in July 1957. Littoral zonation at three main localities (Lüderitz, Elizabeth Bay, and Swakopmund) is briefly described, and an annotated list is presented of the 136 species of marine algae now known from Namibia, as well as of certain algae identified only to genus. Phytogeographically, the marine algal flora of Namibia represents a northward extension of the flora of the western coast of South Africa though somewhat depleted north of the tropic. The boundary between the Namibian flora and the tropical flora of Angola is a sharp one and occurs at, or just north of, the political border of these two countries.

INTRODUCTION

This paper is a further development of reseach originally undertaken as part of the survey of South African intertidal plant ecology then being conducted by Professor William Edwyn Isaac, of the Department of Botany, University of Cape Town. Professor Isaac organized the Namibia field excursion which took place during the southern winter of 1957, in which the participants were Professor W. E. Isaac, Miss Judith Graves, Mr R. H. Simons, and Dr G. W. Lawson. Use has already been made of the collections then assembled in several studies and some of the species identified have been referred to in publications (e.g. John et al., 1979; Lawson, 1978; Lawson & Price, 1969; Lawson et al., 1975; Price et al., 1978, 1986, 1988; Silva, 1959; Simons, 1964, 1966, 1970). It is felt that, despite the time elapsed since the completion of the field work, and despite the rather limited nature of some of our ecological observations in the short time available (which included two successive spring tide periods), a more comprehensive account here attempted is of value in view of the very small amount of work hitherto published on the marine algae of the region and of the current interest in it (see Hommersand, 1986).

The main object of the excursion was to provide data on the composition, distribution, and zonation of the marine algal flora of Namibia (then South West Africa), previously much under-investigated from those points of view. The reason for the lack of information is not far to seek. Along the whole of the coast lies the formidable Namib desert making it difficult to reach and extremely inhospitable. In fact, overland access is only practicable by the roads that have been built to the few townships along the coast. The main accessible areas are around the towns of Swakopmund (22° 40′ S) and Walvis Bay in the centre and Lüderitz (26° 38′ S), some 450 km further south. We also had the opportunity of visiting Elizabethville, a relict town no longer inhabited but accessible by road, a short distance south of Lüderitz. Though the total time available was approximately one month, because of the great distances to be covered between centres and the then indifferent nature of the roads, our main field work was accomplished during about a week when we were based at Swakopmund and a similar period based at Lüderitz. From the phycological point of view the coast of the Republic of South Africa is relatively well-known, having been worked over a considerable number of years (see Seagrief & Troughton, 1973 and Seagrief, 1984). Isaac, (1937*b*) has given a description of the intertidal seaweed vegetation of the west coast of South Africa from Lambert's Bay to the Cape of Good Hope. He has also described zonation to the south-east of the Cape of Good Hope (Isaac, 1949). Though the zonation is similar to that on the west coast, east of Cape Town there are some differences, especially in the sublittoral fringe. In a later paper Isaac & Hewitt (1953) pointed out that the region

from Cape Point to Cape Agulhas is best regarded as an extension of the west coast, if False Bay, which possesses relatively higher sea temperatures, is excepted. It is from the zoological point of view, however, that the most comprehensive picture of the biogeographical distribution of intertidal organisms in South Africa has been constructed. Stephenson and his co-workers were actively engaged on these problems between 1932 and 1937 and these studies were summarized by Stephenson in three papers published in 1939, 1944, and 1948. One of the main conclusions that emerged from this work was that there are three distinct faunas on South African shores: an essentially sub-tropical fauna on the east coast, a warm temperate fauna on the south coast, and a cold temperate fauna on the west coast. There are, of course, many examples of intergrading and overlapping between these faunas. Stephenson indicated his belief that the same situation was substantially true for the algae though it appears from his diagrams (Stephenson, 1944) that the number of species present only along the south coast is relatively small. More recently Bolton (1986) has given a similar but fuller analysis.

From the point of view of the present study it is the distribution of the west coast flora that is most interesting. Its southern limit, as indicated above, is approximately at Cape Agulhas, but the northern limit is less certain, and the establishment of that limit was one of the objectives of the present survey. Stephenson and his co-workers did not penetrate into Namibia and their furthest northerly place studied was the Port Nolloth region, south of the Orange river that marks the coastal boundary between the Cape Province of South Africa and Namibia.

Subsequent to our own work in Namibia, however, Penrith & Kensley (1970*a*, 1970*b*) and Kensley & Penrith (1980) have also visited the area with much the same objectives as ourselves. In their case the interest was mainly zoological and algae were treated as subsidiary. Kensley & Penrith (1973) were also able to study rocky shores at Moçamedes (Angola) and surveys of the marine algae for that same region are reported by Lawson et al. (1975) and John et al. (1981). Information from all these sources, as well as from Wynne (1986), is used in a later section when we attempt to assess the biogeographical significance of our field work in Namibia.

THE NAMIBIAN COAST AND ITS ENVIRONMENTAL CONDITIONS

The long (approximately 1500 km) but relatively straight coastline of Namibia (Fig. 1) lying between 17° 16′ S and 28° 30′ S is inhospitable, the Namib desert reaching directly to the sea along much of its length. Considerable stretches consist merely of wave-beaten beaches and are therefore practically devoid of intertidal seaweed vegetation, though broken rocky outcrops with more extensive areas of cliffs occur at intervals; our observations have been limited to such of these areas as we were able to reach. In general the coast is exposed to the full force of the Atlantic rollers, but some shelter from wave-action is found in places such as the natural harbour at Lüderitz and the artificial one at Swakopmund.

Tides are semi-diurnal and the amplitude is not great, varying most often from under 1.5 m (springs) to little more than one metre (neaps). Exceptionally the range may be over 1.8 m.

Undoubtedly the most significant feature of the Namib coast, as far as seaweeds is concerned, is that the Benguela Current flows northwards along its length with the denser waters of lower temperature closer inshore. The prevailing southerly and south- easterly winds carry these surface waters away from the coast and upwelling of water from 100–300 m depths takes place at most times of the year (Anon., 1964). This causes nutrient-rich waters of low temperature and relatively low salinity to influence the coastal biota. Surface temperatures as low as 10–15°C in winter and 12-20°C in summer for this coast are on record (Anon., 1964), and Isaac (1937*a*) points out that the average annual temperature at Walvis Bay, just within the tropics, is as low as 16.1°C. Bolton (1986) includes 10 year averages of annual maximum and minimum monthly temperatures for both Walvis Bay and Lüderitz. Any botanist visiting this area must be struck by the contrast between the extreme paucity of the terrestrial vegetation on the hot and arid coastal plains and the relative luxuriance of the marine vegetation.

According to Sverdrup, Fleming & Johnson (1942), the effect of the Benguela Current is particularly marked as far north as latitude 17°; thus virtually the whole of the Namib coast is included since the northern border at Kunene River mouth is at 17° 16′ S. Somewhere near Cape Frio (18° 30′ S) the Benguela Current begins to turn out westwards into the Atlantic. More detailed accounts of the hydrography of the region are given in, for example, Anon. (1963), Stephenson & Stephenson (1972), and Richards et al. (1981), while Shannon et al. (1987) describe a mobile front interfacing Angolan waters and the Benguela System. Sand storms on the coastal strip are frequent enough events, but far more common and of greater significance to its desert life are the 'mist-rain' and chilling sea mists that blanket the coast during darkness and early parts of the day (Anon., 1964: 77, 83). These mists are more frequent in the north than in the south. Thus, emersed shore life is perhaps very often shielded from the worst effects of desiccation and overheating during the early part of the mornings. One of the causes of this condensation is the relatively low surface temperature of the adjacent sea (Anon., 1964). Coastal humidity is relatively high even in summer (certainly higher than at Cape Town) and this, too, must have a protective role (Anon., 1964).

PATTERNS OF LITTORAL ZONATION

In the following account we have used the littoral zonation scheme of Lewis (1961). As faunal zonation is important in Lewis' scheme we have, where necessary, added our own limited observations on the vertical distribution of animals.

(a) The Lüderitz area

At Lüderitz we examined littoral rocks at three sites: firstly, the recreational area adjacent to the town itself; secondly, at Elizabeth Bay (visited through the courtesy of the regional representative of Consolidated Diamond Mines) a 'ghost' town about 30 km to the south of Lüderitz, and at one time a centre for diamond operations; lastly, Halifax Bay, on the open coast about 8 km west of Lüderitz.

i) Lüderitz

This site is in the vicinity of the resort area. Since it is a bay within a bay it is well protected from surf action, and waves were never higher than about 0.5 m during our stay.

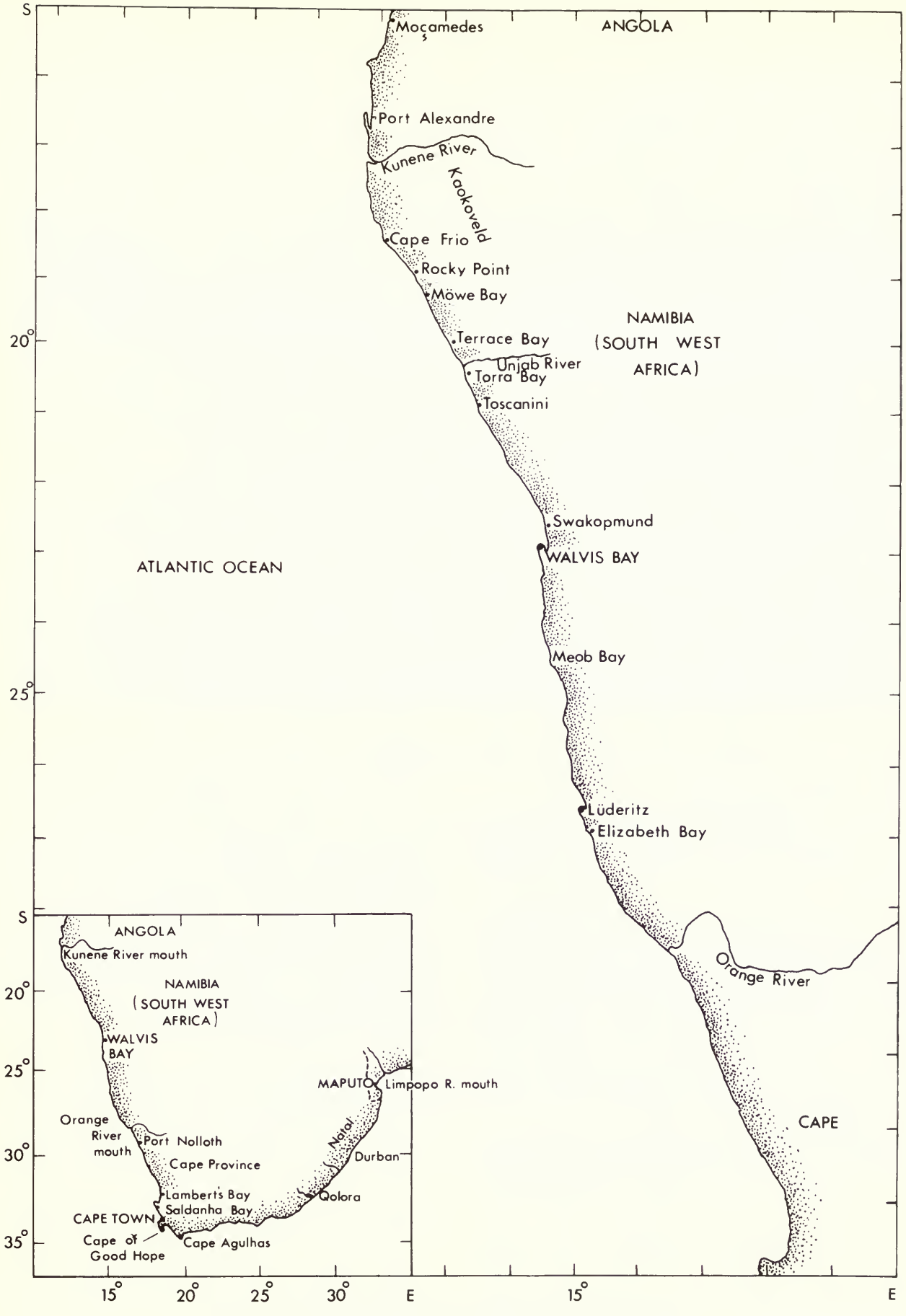

Fig. 1 Map of Namibia to show the localities mentioned in the text.

The Littoral Fringe
The most striking feature of this zone was the abundance of the small snail *Littorina knysnaensis* (Philippi)* everywhere present. Algae were few, mostly scattered plants of *Porphyra capensis* and, in places, a sparse blackish crust of blue-green algae. Species of *Cladophora* were often present in small rock pools.

The Eulittoral
Barnacles were not abundant and there was much bare rock in the upper levels, even on the outer relatively less sheltered rocks. On the innermost sheltered rocks barnacles seemed virtually absent. Penrith & Kensley (1970*a*) do not mention them in their account of the 'rocks below the strand cafe' at Lüderitz and do not include them in any of their figs. 1–4, showing the principal organisms of the localities visited. They do, however, list two barnacles (*Chthamalus dentatus* Krauss and *Balanus algicola* Pilsbry), noting that a few specimens were present in sheltered localities. In our opinion, however, there were sufficient numbers in 1957 to give an indication of the upper limit of the Eulittoral, which was approximately the same as the upper limit of a small brown limpet, *Patella granularis*. The blackish crust of Cyanophyceae present in the Littoral Fringe was more obvious here, interspersed among the barnacles, and it is worth noting that the barnacles themselves often had a greenish tinge, presumably due to epizoic or boring algae. A few *Littorina* also extended downwards among the upper barnacles. It was in this upper Eulittoral zone that the *Porphyra capensis* belt was found below *Littorina* and mixed with the barnacles and brown limpets. *Hildenbrandia rubra* was also found at this level, but only in damp depressions. On some sheltered rocks, *Ulva* formed an ill-defined belt below *Porphyra*.

The next lower algal belt was that of *Nothogenia erinacea*, especially prominent in sheltered places followed by scattered clumps of *Aeodes orbitosa* at the lower limits of *Chthamalus* and of the upper Eulittoral algae.

Below *Aeodes*, no single algal species dominated and the lower part of the Eulittoral was occupied by a mixed, mainly red algal, community, chiefly *Champia lumbricalis, Gigartina stiriata, Gigartina radula,* and *Iridaea capensis,* with some *Cladophora, Polysiphonia,* and articulated and crustose corallines.

Of the animals at lower Eulitttoral levels, limpets were most evident, *Patella granularis* L. penetrated from higher up, to be joined by the larger *Patella granatina* L. at about the same level as *Chthamalus* dropped out, and next by *P. argenvillei* Krauss. This last species extended into the Sublittoral Fringe where *Patella barbara* L. was also present. Forming a striking feature on more sheltered rocks was a thick encrustation of the gritty tubes of the polychaete worm, *Gunnarea capensis* (Schmarda), which continued down to low-water mark. Mussels were present but not common.

The Sublittoral Fringe
A well-marked Sublittoral Fringe was dominated by *Laminaria pallida* and the hollow-stiped *L. schinzii* (but see note below under *L. pallida* in the annotated list of species). Many of the species of the mixed red algal belt of the lower Eulittoral, such as *Champia lumbricalis, Gigartina stiriata, G. radula*, and geniculate and encrusting Corallinaceae, also extended into the Sublittoral Fringe where they were joined by species apparently restricted to that zone, such as *Hypnea* spp. *Hypnea spicifera* was found only locally in the protected shallows of the harbour. *Gracilaria verrucosa* occurred in the drift, and its presence in quantity is reported by Rotmann (1987).

ii) Elizabeth Bay
Very gently sloping rocks in the centre of the rather shallow open bay were studied. Although the outermost rocks were exposed to strong wave-action, those inshore were appreciably sheltered but never as much as the rocks at Lüderitz.

The Littoral Fringe
This level was occupied by rather large individuals of *Littorina knysnaensis*, very common in some places and less frequent in others. *Porphyra capensis* was present to some extent.

The Eulittoral
The upper part of this zone was occupied mostly by limpets (*Patella granularis*), and barnacles were not observed at this level. *Porphyra capensis* occurred sporadically.

Below the *Porphyra* belt but still within the limpet belt, *Aeodes orbitosa*, associated with *Splachnidium rugosum*, was commonly found. At this level *Chordariopsis capensis* was also very frequent but mostly in small pools and often accompanied by *Scytosiphon lomentaria*.

Algae overlapping with this *Aeodes-Splachnidium* belt were *Centroceras clavulatum, Caulacanthus ustulatus*, and occasional plants of *Corallina, Ulva,* and *Codium*. Below these was a belt of *Gunnarea capensis* tubes, sometimes as much as 0.30 m in thickness above the rock surface. Growing on this were several algal species, notably *Ceramium* sp., *Leathesia difformis*, and *Cladophora* sp., the last-mentioned sometimes carrying the *Leathesia*. It should be noted that a second type of worm tube, probably a *Pomatoleios*, was sometimes present. Much harder and smoother than *Gunnarea*, it often supported coralline crusts or tufts of *Gelidium micropterum* and occurred frequently mixed with mussels up to the lower level of *Aeodes*.

Near the lower limit of the *Gunnarea* belt began a belt of *Champia lumbricalis*, often epiphytized by *Aristothamnion collabens*, which extended into the Sublittoral Fringe to form an undergrowth to the kelps. Large limpets, often bearing small barnacles, formed fairly distinct areas interspersed with *Gunnarea* in the lower part of its belt.

The Sublittoral Fringe
This was dominated by *Laminaria pallida* and *Laminaria schinzii* but *Ecklonia maxima* was present especially in pools (Plate 1). Other plants commonly found were *Pachymenia carnosa, Gigartina stiriata, G. radula*, and *Champia lumbricalis*. In addition there were patches of *Petalonia debilis, Centroceras clavulatum, Cladophora* spp., and crustose corallines. Animals included *Patella granatina*, often bearing small barnacles, the red sponge *Hymeniacidon perlevis* (Montagu), and the starfish *Asterina exigua* (Lam.). Some patches of mussels were present but by no means enough to account for the vast quantities of shells thrown up on nearby beaches. *Patella compressa* L. and *Polysiphonia virgata* were found on the stipes of cast-up *Laminaria*.

* The small snail of the littoral fringe was originally identified for us under this name. We note that Penrith & Kensley (1970*a*,1970*b*) and Kensley & Penrith (1980) refer to what is almost certainly the same entity as *Littorina punctata* Philippi. In our opinion, however, these animals and those also referred to as *Littorina punctata* that commonly inhabit the littoral fringe in the Gulf of Guinea are not identical and, to avoid confusion, we have tentatively retained the original name provided.

Plate 1 Kelp beds of the sublittoral fringe exposed at low spring tides at Elizabeth Bay. *Laminaria pallida, Laminaria schinzii*, and *Ecklonia maxima* are present.

iii) Halifax Bay

A very brief visit was made to Halifax Bay where there was a considerable extent of rocky coast and low cliff. Despite some protection from the offshore penguin-populated islands, wave exposure was strong in this area. The species present, and their distribution on the shore, were much more in accord with the typical pattern of zonation found on the west coast of South Africa. Several species not found at Lüderitz itself were conspicuous here. *Splachnidium rugosum* was fairly common in the upper Eulittoral, whilst *Ecklonia maxima* was abundant in the sublittoral kelp beds. This counteracted the impression we had gained from our examination of the rocks near Lüderitz itself that a number of species characteristic of the west coast flora of South Africa had already disappeared at about the latitude of Lüderitz, and indicated that the sheltered conditions of the harbour itself were more likely to be responsible for these apparent absences.

(b) The Swakopmund area

The most northerly locality visited was Swakopmund (22° 40′ S) just within the tropics. Intertidal zonation was examined on the concrete blocks of the harbour wall and at two points south of the town where there were extensive outcrops of beach rock. The contrast between the rich algal flora of the intertidal region and the extremely barren desert lying directly behind the beach was even more marked than at Lüderitz.

i) The harbour wall

The Littoral Fringe

This was occupied by *Littorina knysnaensis*, accompanied by some *Siphonaria capensis*, though more of the latter were found in the Eulittoral. Plants of *Porphyra capensis*, though not extending as high as the snails, were scattered throughout the intertidal.

The Eulittoral

The more wave-exposed south-western faces of the harbour wall could be divided into two subzones, an upper one in which the dominant animals were *Chthamalus dentatus* and *Patella granularis*, and a lower one in which occurred dense carpets of small specimens of the mussel *Perna perna* and large limpets.

In the upper subzone, the main algae found were *Chaetomorpha*, which extended more or less throughout, with *Iridaea capensis* and some *Petalonia debilis* in its lower part. In the upper reaches of the lower Eulittoral subzone, *Polysiphonia*, mixed with occasional plants of *Ulva* and of *Chylocladia capensis*, formed a marked belt. *Iridaea capensis* bridged the upper and lower subzones. The lower part of the lower

Plate 2 *Laminaria schinzii* dominating the sublittoral fringe near the concrete pier at Swakopmund.

Plate 3 *Porphyra capensis* on sheltered rocks behind the concrete pier at Swakopmund.

Eulittoral subzone was occupied by *Chondria capensis* down to the beginning of the *Laminaria* belt.

The Sublittoral Fringe
Due to heavy wave-action it was not possible to investigate this level except to note that it appeared to be dominated by the hollow-stiped *Laminaria schinzii* (Plate 2).

ii) Sheltered rocks behind the pier
The algal distribution was very different here, being less distinct due to the broken nature of the rocks; good shelter from strong surf also meant that the algae were telescoped into the lower part of the Eulittoral. *Enteromorpha* was a conspicuous feature, sometimes accompanied by *Urospora* sp. on the upper parts of the rocks. *Porphyra capensis* was also very common (Plate 3), though not attaining quite the same height up the shore as did the green algae. Cyanophyceae were also spread over the rocks, especially in the form of a blackish powdery covering. The animals most in evidence were *Littorina knysnaensis* and mussels (*Modiolus* sp.), though our collections also included *Balanus algicola, Siphonaria capensis* Quoy & Gaimard, and *Patella granularis*.

iii) Rocks south of Swakopmund
Our study of two fairly extensive and irregular outcrops of gently-sloping rock, interrupting the sandy beaches, yielded the following information.

The Littoral Fringe
This zone was present only where the rocks stood high enough to accommodate it. *Littorina knysnaensis* was again the dominant organism though it occurred also well down into at least the middle of the Eulittoral zone. *Porphyra capensis* was present in fairly large quantity, forming a narrow band which did not appear to extend downwards as at some other localities; not all samples taken could be attributed with certainty to *P. capensis* since there were puzzling variants, especially among the smaller forms; in particular we draw attention to a small form with a distinctive rounded margin (Plate 4), possibly an undescribed species. We also collected *Siphonaria* sp. and a black and white limpet from the *Porphyra* belt; at a somewhat lower level small plants of *Ulva* were present, mainly in depressions.

The Eulittoral
Barnacles and the small brownish *Patella granularis* with some *Littorina knysnaensis* occupied the upper portion of this zone; algae were few but included some *Chaetomorpha*, mostly confined to shallow pools, and scattered small plants of *Ulva*.

Near the middle a subzone was discernable; mussels began to replace barnacles, especially on the somewhat more exposed parts where the former were generally rather larger; *Patella granularis*, however, extended down into the mussel subzone, where it was joined by some of the larger limpet species. The upper limit of mussels and large limpets marked the beginning of a much greater algal cover in the upper part of the subzone (Plate 5), forming a distinct girdle of red algae of which *Caulacanthus ustulatus* and *Gymnogongrus glomeratus* were the chief components with *Nothogenia erinacea,*

Plate 4 Plants of a small form of *Porphyra* found at Swakopmund.

Plate 5 The Eulittoral zone on rocks south of Swakopmund. Note that the upper part is very arid and practically devoid of algae, whereas the lower part is covered by a dense mat of mixed algae including *Caulacanthus ustulatus, Gymnogongrus glomeratus*, and *Centroceras clavulatum*.

Chylocladia capensis, Acrosorium maculatum, and much *Centroceras clavulatum*, which often occurred epiphytically on the *Caulacanthus*.

Below this *Caulacanthus-Gymnogongrus* girdle was another slightly less distinct belt dominated by *Chondria capensis*, but including *Pterosiphonia cloiophylla, Ralfsia expansa, Cladophora* spp.,and, continuing into the Sublittoral, geniculate and crustose corallines.

The lowermost parts of the Eulittoral bore, in addition, a number of larger red algae, perhaps representing elements of the Sublittoral Fringe flora though rising above the *Laminaria* level. They included species of *Plocamium*, such as *P. cornutum* and *P. rigidum*, as well as the large fleshy fronds of *Pachymenia carnosa*. (Plate 6) and *Aeodes orbitosa* (Plate 7).

The Sublittoral Fringe

This final zone was dominated by *Laminaria schinzii* but included many of the algae found in the lower parts of the Eulittoral—corallines, *Plocamium* spp., and *Pachymenia*, which together formed an undergrowth to the kelps. We did not find *Ecklonia maxima*. The dominance of *L. schinzii* was also indicated by the large quantity of this species thrown up on nearby beaches.

c) General comments

The general features of algal zonation in the Lüderitz area are similar to those of the South African coast as described by Isaac (1937*b*). Both areas have an upper *Porphyra* belt. This is followed downwards by a *Nothogenia* belt, which at Lüderitz consists of *N. ovalis*, though this belt did not seem to be represented at Elizabeth Bay. An *Aeodes orbitosa* belt was also present at both Lüderitz and at Elizabeth Bay. *Aeodes* was accompanied by *Splachnidium rugosum* and *Chordariopsis capensis*. *Bifurcaria brassicaeformis* was apparently altogether absent from Namibia. A *Champia lumbricalis* belt, accompanied by species of *Gigartina* and *Iridaea capensis*, at Lüderitz was also present at Elizabeth Bay; *Iridaea* thus appears to be somewhat lower on the shore here than further south where it occurs in the *Aeodes* belt. Finally, a kelp belt is present at all localities, with *Laminaria pallida* and a hollow-stiped form identified as *L. schinzii* found everywhere. One of us (R.H.S.) has established that similar hollow forms dominate the sublittoral as far south as Cape Columbine, the western headland of St. Helena Bay about 120 km north of Cape Town. *Ecklonia maxima* was also present at all localities, except for the sheltered shores at Lüderitz, but usually as a small plant. Where present, epiphytes seemed to prefer *Ecklonia maxima* to *Laminaria schinzii*; *Laminaria pallida* was usually without epiphytes. On the west coast of South Africa, *Suhria vittata* occurs mostly associated with *Ecklonia maxima* but in the Lüderitz region it was often found on rocks as well as on limpets in the intertidal.

Northwards, at Swakopmund, the situation was noticeably different. The algal belts appeared to be narrower and lower

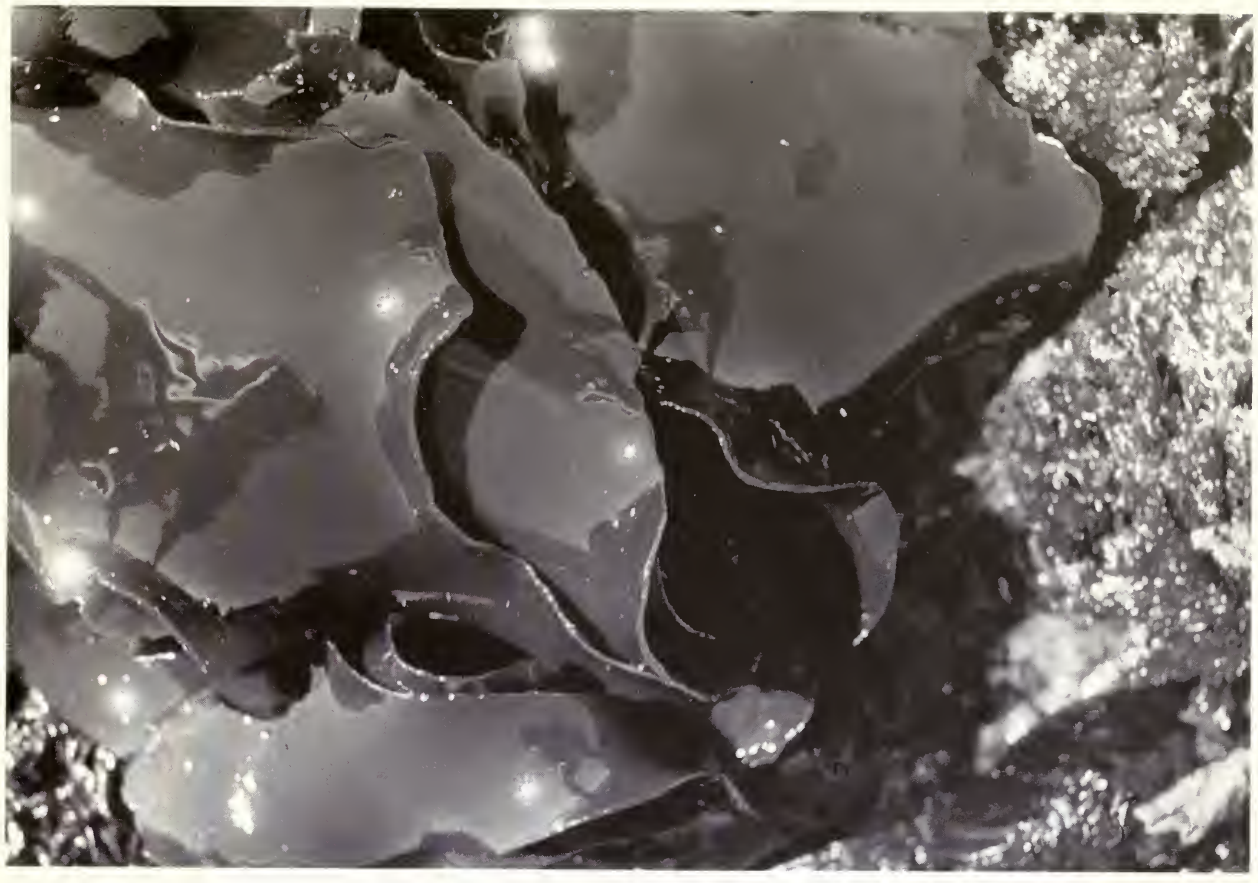

Plate 6 *Pachymenia carnosa* growing on rocks just south of Swakopmund.

on the shore in this area than they were further south. Both the *Porphyra* and the *Nothogenia* belts were present, at least on the rocks south of Swakopmund. The *Aeodes* belt was not represented here though *Iridaea capensis* was recorded from the harbour wall at an appropriate level. Isaac's *Champia-Gigartina* belt was much modified: *Champia lumbricalis* was present in limited quantity, but the larger species of *Gigartina* (*G. stiriata, G. radula*, and *G. scutellata*) were not found at all. Finally, in the kelp bed *Ecklonia maxima* had, so far as we could ascertain, completely disappeared and *Laminaria schinzii*, rather than *L. pallida*, appeared to be dominant.

THE PHYTOGEOGRAPHICAL STATUS OF THE NAMIBIAN MARINE ALGAL FLORA

The biogeographical status of the marine flora and fauna of the western coast of southern Africa has been a somewhat controversial topic since the biota have been regarded by some authors as cold temperate and by others as warm temperate. Stephenson (e.g. 1948) was the leading proponent of the former view and in this he was followed by Hedgpeth (1957) who, largely on the basis of a synthesis by Ekman (1953), produced a map of the littoral zoogeographic provinces of the world. In this map Hedgpeth placed a cold temperate zone on the western side of southern Africa directly abutting on to, and indeed overlapping with, the tropical zone of western Africa. In all other regions of the world he had indicated a warm temperate zone lying between the cold temperate and tropical zones. Others who followed this view were Knox (1960) and Michanek (1979). Ekman (1953) regarded the region in question as warm temperate, as did Briggs (1974), Bolton (1986), Hoek (e.g. 1984), and Lüning (1985). It should be noted that the question is seen from different standpoints by different authors; thus Ekman, Briggs, and Hedgpeth were concerned soley with animal distributions, whereas Bolton, Hoek, and Lüning dealt with plants. Stephenson took both into account. Again, Stephenson was concerned only with intertidal organisms and his boundaries are decidedly sharper than those produced by some other authors, who included consideration of the deep sublittoral where distributions show fewer differences between east and west. This is due to the fact, as pointed out by Brown & Jarman (1978), that sea temperatures are much less variable in deeper waters, ranging from only about 12–14°C throughout the year from Lüderitz on the west coast to Port Elizabeth in the east. The subject is well reviewed by Brown & Jarman (1978) who adhered to the Stephenson viewpoint, and by Bolton (1986) who takes the opposite line; it is also mentioned by John & Lawson (1989) and Lawson (1988).

Bolton (1986) points out that Stephenson (1948) considered large stands of kelps to indicate cold temperate conditions, as in the northern hemisphere. Had Stephenson realized that *Ecklonia maxima* and *Laminaria pallida* under

Plate 7 *Aeodes orbitosa* growing over encrusting corallines on the pier at Swakopmund.

laboratory conditions actually grow best at higher temperatures than most other kelps (17.5–20°C for optimal gametophyte growth for the former and 15°C for the latter), he might have concluded differently. Similarly, *Macrocystis angustifolia* has an optimum for gametophytic growth at 14.16°C and 17.5°C for reproduction (Branch, 1974). But it should perhaps be borne in mind that temperatures which are optimal for growth in the laboratory do not always necessarily reflect what actually happens in nature. The figures given by Bolton (1986), for instance, indicate that *Ecklonia* occurs on parts of the west coast of South Africa where the mean temperature for the warmest month does not rise much above 13°, which is well below the temperatures for optimum growth given above. Further possible support for the warm temperate view, however, is given by Lawson (1988), who has suggested, on the basis of ordination, that the marine flora of the western side of southern Africa has more in common with those of Uruguayo-Bonaerense and Uruguay in South America than with that of the more strictly cold temperate one of Patagonia (see Kühnemann, 1972). If this is indeed a warm temperate marine climate continuous with that of the south coast of South Africa how may the biotic discontinuity that exists between the two be explained? A possible reason to explain the somewhat anomalous situation where two largely different warm temperate floras lie adjacent to one another without completely mixing, may be that mean sea temperatures along the south coast are generally appreciably higher than those of the west coast and also show a wider range between coldest and warmest months (see fig. 2 in Bolton, 1986).

Table 1 Distribution of the Namibian marine algal flora within and to the north and south of Namibia. The species are arranged in a geographical sequence.

Species	Angola	Namibia North	Namibia Centre	Namibia South	South Africa West	South Africa South and south-east
Codium decorticatum	+	+	+			
Ulva uncialis	+		+	+		
Enteromorpha linza	+		+	+	+	
E. compressa	+		+		+	
Caulacanthus ustulatus	+	+	+	+	+	+
Centroceras clavulatum	+	+	+	+	+	+
Gracilaria verrucosa	+	+	+	+	+	+
Plocamium suhrii	+	+				+
Acrosorium maculatum	+		+	+	+	+
Bryopsis plumosa	+		+	+	+	+
Hypnea musciformis	+		+			+
Ulva fasciata	+		+			+
Grateloupia filicina	+			+	+	+
Colpomenia sinuosa	+			+		+
Enteromorpha tubulosa		+				
Gigartina teedii		+	+			
Cladophora capensis		+	+	+	+	
C. contexta		+	+	+	+	
C. flagelliformis		+	+	+	+	
C. mirabilis		+	+	+	+	
Laminaria schinzii		+	+	+	+	
Aristothamnion collabens		+	+	+	+	
Ceramium atrorubescens		+	+	+	+	
Gymnogongrus complicatus		+	+	+	+	
G. dilatatus		+	+	+	+	
G. vermicularis		+	+	+	+	
Hildenbrandia rubra		+	+	+	+	
Kallymenia schizophylla		+	+	+	+	
Pachymenia carnosa		+	+	+	+	
Phyllymenia belangeri		+	+	+	+	
Polysiphonia urbana		+	+	+	+	
Suhria vittata		+	+	+	+	
Nothogenia ovalis		+	+	+	+	
Chaetomorpha robusta		+	+		+	
Streblocladia camptocladia		+	+		+	
S. fasciculifera		+			+	
Hypnea ceramioides		+			+	
Codium fragile		+	+	+	+	+
Ralfsia expansa		+	+	+	+	+
Ceramium arenarium		+	+	+	+	+
Chondria capensis		+	+	+	+	+
Gymnogongrus glomeratus		+	+	+	+	+
Iridaea capensis		+	+	+	+	+
Nothogenia erinacea		+	+	+	+	+
Plocamium rigidum		+	+	+	+	+
Porphyra capensis		+	+	+	+	+
Pterosiphonia cloiophylla		+	+	+	+	+
Aeodes orbitosa		+	+	+	+	+
Ceramium flaccidum		+		+	+	+
Hypnea spicifera		+		+	+	+
Platysiphonia miniata		+		+	+	+
Acrosorium acrospermum		+	+		+	+
Ceramium diaphanum		+	+		+	+
Heringia mirabilis		+	+		+	+
Tayloriella tenebrosa		+	+		+	+
Bryopsis caespitosa		+			+	+
Hincksia confervoides		+			+	+
Plocamium corallorhiza		+			+	+
P. vulgare		+			+	+
Gelidium pristoides		Unspecified			+	+
Codium duthieae		+	+	+		+
Enteromorpha prolifera		+				+
Endarachne binghamiae		+				+
Arthrocardia palmata		+				+
Hypnea ? tenuis		+				+
Ulva nematoides			+			
Hincksia granulosa			+			

Table 1 cont.

Species	Angola	Namibia North	Namibia Centre	Namibia South	South Africa West	South Africa South and south-east
Acrosorium cincinnatum			+			
Antithamnion leptocladum			+			
Audouinella hypneae			+			
Cryptonemia hibernica			+			
Cryptopleura calophylloides			+			
Epymenia capensis			+			
Erythrotrichia welwitschii			+			
Gelidium pusillum			+			
Iridaea elongata			+			
Lomentaria patens			+			
Nothogenia magnifica			+			
Ophidocladus simpliciusculus			+			
Rhodophyllis reptans			+			
Schottera nicaeensis			+			
Stylonema alsidii			+			
Enteromorpha atroviridis			+	+	+	
E. bulbosa			+	+	+	
Chordariopsis capensis			+	+	+	
Laminaria pallida			+	+	+	
Carpoblepharis flaccida			+	+	+	
Ceramium obsoletum			+	+	+	
C. planum complex			+	+	+	
Epymenia obtusa			+	+	+	
Gigartina bracteata			+	+	+	
G. radula			+	+	+	
Polysiphonia virgata			+	+	+	
Schizymenia obovata			+	+	+	
Ulva capensis			+		+	
Papenfussiella gracilis			+		+	
Callithamnion hookeri			+		+	
Carpoblepharis minima			+		+	
Gymnogongrus corymbosa			+		+	
Haraldiophyllum bonnemaisonii			+		+	
Rhodymenia linearis			+		+	
Petalonia debilis			+	+	+	+
Chylocladia capensis			+	+	+	+
Plocamium cornutum			+	+	+	+
P. glomeratum			+		+	+
Streblocladia corymbifera			+		+	+
Chaetomorpha linum			+			+
Heterosiphonia dubia			+			+
Rhodymenia natalensis			+			+
Arthrocardia carinata				+		
Derbesia lamourouxii				+		
Actinococcus latior				+		
Euhymenia schizophylla				+		
Herposiphonia heringii				+		
Bryopsis tenuis				+	+	
Codium isaacii				+	+	
Desmarestia firma				+	+	
Ecklonia maxima				+	+	
Scytosiphon lomentarius				+	+	
Arthrocardia filicula				+	+	
A. setchellii				+	+	
Botryocarpa prolifera				+	+	
Botryoglossum platycarpum				+	+	
Champia lumbricalis				+	+	
Delesseria papenfussii				+	+	
Gelidium micropterum				+	+	
Gigartina scutellata				+	+	
Hymenena venosa				+	+	
Pleonosporium harveyanum				+	+	
Polyopes constrictus				+	+	
Polysiphonia atrorubescens				+	+	
Trematocarpus flabellatus				+	+	
Leathesia difformis				+	+	+
Splachnidium rugosum				+	+	+
Gigartina stiriata				+	+	+

The list of species given below incorporates all known records and contains 136 identified species whose known distributions on southern African shores are displayed in Table 1, as well as at least 35 taxa assigned only to genera. It is evident that most (97) Namibian seaweeds occur also on the west coast of South Africa: even in the north of Namibia 44 species out of 57 identified plants are species that occur on the west coast of South Africa with 21 endemics involved; the other two segments, namely central (Swakopmund area) and south (Lüderitz area), contain respectively 89 and 83 identified species. An interesting point is that whereas about 74% of all the taxa present in the south segment are common with the west coast of South Africa, the comparative figure for the central segment is only 62%—in fact, Swakopmund is notable for having 20 (22% of the total identified) species apparently not occurring on the west coast of South Africa. By contrast elements of the Angolan seaweed flora are remarkable for their very poor representation—14 in all, with eight of these of very wide distribution or even cosmopolitan.

The overall concept of the Namibian seaweed flora that emerges is of an attenuating northward extension of the flora of the west coast of South Africa that abruptly terminates somewhere near the border with Angola. Less noticeable, but nevertheless significant, is the change of species composition at Swakopmund. Others have also observed biotic changes in that vicinity, for instance, a reduction in frequency of the Cape rock lobster, *Jasus lalandii*, north of 25°S (Pollock & Beyers, 1981). A possible explanation for these changes is that the relative wind stress and concomitant water circulation is reduced here and to the north (Agenbag & Shannon, 1988).

Table 1 shows discontinuities that seem somewhat anomalous. Thus *Grateloupia filicina*, for example, is apparently absent between the Kunene River mouth and Lüderitz, and *Colpomenia sinuosa* is recorded only in the Lüderitz area of Namibia while being present in Angola and the southern Cape. Again *Aeodes orbitosa*, and some othe species such as *Ceramium flaccidum*, have been found all the way from northern Namibia to the southern coast of Africa except at Swakopmund. Two possible reasons for these anomalies are that there have been misidentifications and/or inadequate collection since it is somewhat presumptuous to discuss discontinuities of distribution on the rather meagre data available. It is hoped, however, that this presentation will serve as a useful check-list for further studies of the respective floras.

ANNOTATED LIST OF SPECIES

The Western African seaweed checklists of Lawson & Price (1969) and Price et al. (1978, 1986, 1988) cite unpublished lists prepared by one of us (R.H.S.). These lists include the specimens collected on the trip with which this paper is concerned, together with identifications of algae collected by Penrith & Kensley, and other miscellaneous records from Namibia. We have included all these in the list that follows and have added all earlier records of marine algae from this coast as well as algae mentioned by Penrith & Kensley (1970 *a* & *b*), Kensley & Penrith (1973, 1980) and the recent identifications by Wynne (1986). Where records of other authors are cited an asterisk(*) indicates that we have been able to confirm independently the presence of the species in question at the given locality. Sites may be identified by the following letters:

AB—Agate Beach, AF—Angra Fria, CF—Cape Frio (and False Cape Frio), D—Diaz Point (Lüderitz area), EB—Elizabeth Bay, FB—Flesh Bay, G—Grossebucht, HB—Halifax Bay, HL—Honolulu (near Kunene River mouth), K—Kaokoveld, KR—Kunene River, L—Lüderitz, MB—Mowe Bay, N—Namibia (used when locality is not mentioned), RP—Rocky Point, S—Swakopmund, TB—Torra Bay, TC—Terrace Bay, TS—Toscanini, U—Unjab, WB—Walvis Bay.

Specimens are deposited in BOL, the Herbarium of the Department of Botany, University of Cape Town.

CHLOROPHYCEAE

Bryopsis caespitosa Suhr ex Kütz. MB

Bryopsis plumosa (Huds.) Agardh EB, N (Lawson & Price, 1969), S.

Bryopsis tenuis Levr. L, ?N (Lawson & Price, 1969).

Bryopsis spp. EB, L, RP, S, TB, TC.

Chaetomorpha aerea (Dillwyn) Kütz. see *Chaetomorpha linum.*

Chaetomorpha linum (O. F. Müll.) Kütz. S (Wynne, 1986, as *C.aerea)**.

Chaetomorpha robusta (Aresch.) Papenf. MB, RP, S, TB, TC.

Chaetomorpha spp. D, S, TB.

Cladophora capensis (Agardh) De Toni D, EB, HB, L (Penrith & Kensley, 1970*a*)*, MB, RP (Penrith & Kensley, 1970*b*)*, S, TB, TC.

Cladophora contexta Levr. EB, L, MB, S.

Cladophora flagelliformis (Suhr) Kütz. EB, S (Wynne, 1986)*, TB, L.

Cladophora mirabilis (Agardh) Rabenh. CF (Kensley & Penrith, 1980), KR (Kensley & Penrith, 1980), L, N (Lawson & Price, 1969), RP, S (Wynne, 1986)*, TB, TC.

Cladophora virgata (Agardh) Kütz. see *Cladophora flagelliformis.*

Cladophora sp. EB.

Codium decorticatum (Woodw.) M. Howe MB, N (Lawson & Price, 1969), RP, S (Silva, 1960; Wynne, 1986)*.

Codium duthieae P. C. Silva L, MB, ?N (Lawson & Price, 1969), RP (Penrith & Kensley, 1970*b*), S.

Codium fragile subsp. *capense* P. C. Silva D, EB, L (Penrith & Kensley, 1970*a*, Silva, 1959), N (Lawson & Price, 1969; Schmidt, 1923—as *C.fragile*), RP, S (Silva, 1959; Wynne, 1986)*, TB, U.

Codium isaacii P. C. Silva L (Silva, 1959), N (Lawson & Price, 1969).

Codium sp. S.

Derbesia lamourouxii (J. Agardh) Solier L.

Enteromorpha atro-viridis (Levr.) Wynne G, L (Penrith & Kensley, 1970*a*—as *Ulva atroviridis**), S (Wynne, 1986).

Enteromorpha bulbosa (Suhr) Kütz. EB, S.

Enteromorpha compressa (L.) Grev. S.

Enteromorpha linza (L.) J. Agardh L, S.

Enteromorpha prolifera (O. F. Müll.) J. Agardh MB, RP.

Enteromorpha tubulosa Kütz. RP.

Enteromorpha spp. AF (Kensley & Penrith, 1980), CF (Kensley & Penrith, 1980), HB, L, N (Lawson & Price, 1969), S.

Ulva atroviridis Levr. see *Enteromorpha atro-viridis.*

Ulva capensis Aresch. MB, L, S (Wynne, 1986).
Ulva fasciata Delile S.
Ulva nematoidea Bory S (Wynne 1986)*.
Ulva uncialis (Kütz.) De Toni L (Pilger, 1908—as *U. uncialis Suhr*), MB, N (Dinter, 1928—as *Ulva capensis*; Lawson & Price, 1969).
Ulva spp. EB, L, MB, N (Lawson & Price, 1969), RP, S, TB, TC, U.
Urospora sp. S.

PHAEPHYCEAE

Chordaria flagelliformis (O. F. Müll.) Agardh N (Dinter, 1919)—probably *Chordariopsis capensis* according to Price et al. (1978).
Chordariopsis capensis (Agardh) Kylin CF (Kensley & Penrith, 1980)*, EB, L (Penrith & Kensley, 1970*a*)*, N (Price et al., 1978), RP, S (Wynne, 1986)*, TB.
Colpomenia sinuosa (Roth) Derb. & Sol. AB, D, EB, N (Price et al., 1978).
Desmarestia firma (Agardh) Skottsb. L (Price et al., 1978). See notes in Price et al. (1978) on this entity.
Ecklonia maxima (Osbeck) Papenf. EB, HB, L, N (Price et al., 1978), S (Wynne, 1986—'in the drift'. Wynne also mentions that his species occurs at RP and cites a letter from Kensley on this, but we have not been able to find it referred to in Penrith and Kensley [1970*b*]).
Ectocarpus spp. N (Price et al., 1978), RP, S.
Endarachne binghamiae J. Agardh RP.
Hincksia granulosa (Smith) P. C. Silva S (Wynne, 1986—as *Giffordia granulosa*).
Laminaria digitata forma *ensifolia* (Kütz.) Foslie N (Dinter, 1922), WB (Foslie, 1893). See note in Price et al. (1978).
Laminaria ochroleuca Bach. Pyl. N (Delf & Michell, 1921). See note in Price et al. (1978).
Laminaria pallida Grev. EB, L, N (Delf & Michell, 1921; Price et al., 1978; Schmidt & Gerloff, 1957). WB (Delf & Michell, 1921). It should be noted that some doubt attaches to the presence of *L. pallida* in the Lüderitz area since differences between *L. pallida* and *L. schinzii* are not clear cut and juvenile and inshore plants of the latter often have solid stipes.
Laminaria schinzii Foslie EB, L, MB, N (De Toni, 1895; Dinter, 1922; Feldmann, 1946; John et al., 1981; Lawson et al., 1975; Price et al., 1978; Pilger, 1908; Schmidt & Gerloff, 1957), RP (Penrith & Kensley, 1907*b*)*, S (Wynne, 1986)*, TC, WB (Barton, 1893; Foslie, 1893).
Laminaria sp. L (Penrith & Kensley, 1970*a*).
Leathesia difformis (L.) Aresch. D, EB, L, N (Price et al., 1978).
Myriogloia sp. EB, N (Price et al., 1978), S.
Papenfussiella gracilis Kylin N (Price et al., 1978), S.
Petalonia debilis (O. F. Müll.) Kuntze EB, N (Price et al., 1978), S.
Ralfsia expansa (J. Agardh) J. Agardh CF, EB, N (see note in Price et al. [1978]), S.
Ralfsia sp. KR (Kensley & Penrith, 1980).
Scytosiphon lomentaria (Lyngbye) Link EB, L, N (Price et al., 1978).
Splachnidium rugosum (L.) Grev. EB, G, HB, L (Penrith & Kensley, 1970*a*)*, N (Price et al., 1978).
?Zonaria tempta HB, N (see note in Price et al. [1978]).

RHODOPHYCEAE

Acrosorium acrospermum (J. Agardh) Kylin RP, TB, TC, TS, N (Price et al., 1986), S.
Acrosorium cincinnatum Wynne S (Wynne, 1986), N (Price et al., 1986)*.
Acrosorium maculatum (Kütz.) Papenf. L, S, N (Lawson et al., 1975; Price et al., 1986).
Acrosorium sp. L, MB, S, TB, TC, N (Price et al., 1986).
Actinococcus latior Schmitz L (Pilger, 1908), N (Price et al., 1978), WB (Dinter, 1917).
Aeodes orbitosa (Suhr) Schmitz AF (Kensley & Penrith, 1980), D, EB, CF, (Kensley & Penrith, 1980), G, HB, KR (Kensley & Penrith, 1980), L (Penrith & Kensley, 1970*a*)*, MB, (Penrith & Kensley, 1970*b*), N (Price et al., 1986), RP, U.
Aeodes sp. N (Price et al., 1986).
Antithamnion leptocladum (Mont.) Wynne S (Wynne, 1986), N (Price et al., 1986).
Antithamnion sp. L, RP, N (Price et al., 1986).
Aristothamnion collabens (Rudolphi) Papenf. EB, G, HB, L, N (Dinter, 1918—as *A. purpuriferum*; Price et al., 1986), S (Wynne, 1986)*, TC.
Arthrocardia attenuata Manza see *Arthrocardia palmata*.
Arthrocardia carinata (Kütz.) Johansen L (Pilger, 1908—as *Corallina carinata*), N (Price et al., 1986), S.
Arthrocardia filicula (Lam.) Johansen in Seagrief L, N (Price et al., 1986).
Arthrocardia palmata (Ellis & Sol.) Aresch. MB, N (Price et al., 1986, as *Arthrocardia attenuata*).
Arthrocardia setchellii Manza L.
Arthrocardia sp. D, L (Penrith & Kensley, 1970*a*)*, RP (Penrith & Kensley, 1970*b*)*, TB, N (Price et al., 1986), TC.
Audouinella hypneae (Børgesen) G. W. Lawson & D. John S (Wynne, 1986), N (Price et al., 1986).
Bostrychia moritziana (Sonder ex Kütz.) J. Agardh N (Post, 1963; Price et al., 1986).
Botryocarpa prolifera Grev. EB, L, N (Price et al., 1986).
Botryoglossum platycarpum (Turner) Kütz. EB, L (Simons, 1974; Price et al., 1986).
Callithamnion hookeri (Dillwyn) Gray S (Wynne, 1986), N (Price et al., 1986).
Carpoblepharis flaccida (Agardh) Kütz. L (Pilger, 1908)*, N (Price et al., 1986), S, WB (Delf & Michell, 1921).
Carpoblepharis minima Bart. N (Dinter, 1918; Price et al., 1986), S (Wynne, 1986).
Carpoblepharis sp. N (Price et al., 1986), S.
Carradoria virgata (Agardh) Kylin see *Polysiphonia virgata*.
Caulacanthus ustulatus (Mert.) Kütz. EB, L, MB, N (Price et al., 1986; Searles, 1968), RP, S (Wynne, 1986)*, TB.
Caulacanthus sp. N (Price et al., 1986), TB.
Centroceras clavulatum (Agardh) Mont. D, EB, L (Pilger, 1908)*, MB, N (Price et al., 1986; Searles, 1968), RP, S (Wynne, 1986)*, TB, TC.
Ceramium arenarium Simons L (Simons, 1966), N (Price et al., 1986; Simons, 1966), S (Wynne, 1986), TB.
Ceramium atrorubescens Kylin L (Simons, 1966), S Simons, 1966, Wynne, 1986), TB, N (Price et al., 1986), U, WB (Simons, 1966).
Ceramium capense Kütz. see *Ceramium obsoletum*.
Ceramium diaphanum (Lightf.) Roth TB (Dinter, 1919; Price et al., 1986), WB (Delf & Michell, 1921).
Ceramium flaccidum (Kütz.) Ardiss. G (Simons, 1966, as

Ceramium papenfussianum) HB, HL, KR, L, N (Price et al., 1986, as *Ceramium papenfussianum*).
Ceramium obsoletum† Agardh EB (Simons, 1966), L (Simons, 1966), N (Dinter, 1917; Price et al., 1986 as *C.capense*), WB (Delf & Michell, 1921 as *C.obsolatum*) (= *Microcladia capense* Papenf.
Ceramium papenfussianum Simons See *Ceramium flaccidum.*
Ceramium planum complex sensu Simons 1968 L, N (Price et al., 1986), S (Wynne, 1986).
Ceramium spp. S (Wynne, 1986), TC, TS, N (Price et al., 1986).
Chaetangium erinaceum (Turner) Papenf. see *Nothogenia erinacea.*
Chaetangium magnificum Pilger see *Nothogenia magnifica.*
Chaetangium ornatum (L.) Kütz. see *Nothogenia erinacea.*
Chaetangium ovale (Suhr) Papenf. see *Nothogenia ovalis.*
Champia lumbricalis (L.) Desv. AB, D, EB, G, L (Penrith & Kensley, 1970*a*; Simons, 1974), N (Price et al., 1986).
Chondria capensis (Harvey) Falkenb. CF, L, MB, N (Delf & Michell, 1921; Lawson et al., 1975; Price et al., 1986; Round, 1981; Schmidt & Gerloff, 1967; Simons, 1974), RP, S (Wynne, 1986)*, WB (Dinter, 1919) TB, TC.
Chondria sp. CF (Kensley & Penrith, 1980), KR (Kensley & Penrith, 1980), N (Price et al., 1986).
Chylocladia capensis Harvey L, N (Price et al., 1986), S.
Chylocladia sp. KR, N (Price et al., 1986), RP, TC.
Corallina carinata Kütz. see *Arthrocardia carinata.*
Corallina sp. (Cornicullariae) MB.
Corallina spp. S (Wynne, 1986), RP, N (Price et al., 1986), S, TB, TS.
Cryptonemia hibernica Guiry & L. Irvine N (Price et al., 1986), S (Wynne, 1986).
Cryptopleura calophylloides (J. Agardh) Wynne N (Price et al., 1986), S (Wynne, 1986).
Delesseria papenfussii Wynne EB, N (Price et al., 1986).
Epymenia capensis (J. Agardh) Papenf. N (Dinter, 1926; Schmidt & Gerloff, 1957, as *Rhodymenia capensis* Price et al., 1986), WB (Delf & Michell, 1921, as *Epymenia stenoloba*).
Epymenia obtusa (Grev.) Kütz. EB, L (Pilger, 1908)*, N (Delf & Michell, 1921, Price et al., 1986, Simons, 1974), S (Wynne, 1986)*, TC.
Erythrotrichia welwitschii (Rupr.) Batters S.
Euhymenia schizophylla Kütz. L (Pilger, 1908), N (Price et al., 1986).
Gelidium micropterum Kütz. EB, L, N (Price et al., 1986).
Gelidium pristoides (Turner) Kütz. N (Price et al., 1986).
Gelidium pusillum (Stackh.) Le Jolis N (Price et al., 1986), S.
Gelidium spp. MB, N (Price et al., 1986), RP.
Gigartina bracteata (Gmelin) Setch. & N. Gardner HB, S (Wynne, 1986).
Gigartina radula (Esper) J. Agardh AB, D, EB, HB, L (Penrith & Kensley, 1970*a*)*, S, TC.
Gigartina scabiosa (Kütz.) Papenf. see *G.scutellata.*
Gigartina scutellata (Hering) Simons EB, L, N (Price et al., 1988).
Gigartina stiriata (Turner) J. Agardh D, EB, G, L (Penrith & Kensley, 1970*a*)*, N (Price et al., 1988).
Gigartina teedii (Roth) Lamouroux N (Dinter, 1921; Price et al., 1988), RP, S (Wynne, 1986).

† The plant to which the name *Ceramium obsoletum* Agardh has been applied is apparently unnamed since the *Ceramium capense* cited by Simons (1966: 164) is not congeneric with *Ceramium*.

Gigartina spp. N (Price et al., 1988), RP (Penrith & Kensley, 1970*b*)*.
Gracilaria verrucosa (Huds.) Papenf. L (Rotmann, 1987), N (Isaac, 1956; Michanek, 1971, 1975; Price et al., 1988) S (Wynne, 1986)*, TC, WB.
Grateloupia filicina (Wulf.) J. Agardh EB, HB, L, N (Price et al., 1988).
Griffithsia confervoides Suhr (including *G. cymosa* Simons) MB, N (Price et al., 1988), TB, TC, TS.
Gymnogongrus complicatus (Kütz.) Papenf. L, MB, N (Price et al., 1988), S (Wynne, 1986)*, TB, TC, TS.
Gymnogongrus corymbosus J. Agardh N (Price et al., 1988), S (Wynne 1986).
Gymnogongrus dilatatus (Turner) J. Agardh L (Pilger, 1909)*, N (Price et al., 1988), S (Wynne, 1986)*, TC.
Gymnogongrus glomeratus J. Agardh AB, AF (Kensley & Penrith, 1980), EB, D, L (Penrith & Kensley, 1970*a*)*, N (Kensley & Penrith, 1980; Price et al., 1988), RP (Penrith & Kensley, 1970*b*), S (Wynne, 1986)*, TC, TS.
Gymnogongrus vermicularis (Agardh) J. Agardh CF, HB, KR, L, MB, N (Price et al.,1988), S, TC, TS.
Gymnogongrus spp. G, KR, MB, N (Price et al., 1988), S.
Haraldiophyllum bonnemaisonii (Grev.) Zinova prox. S (Wynne, 1986).
Heringia mirabilis (Agardh) J. Agardh S (Wynne, 1986), TC.
Heringia sp. MB.
Herposiphonia heringii (Harvey) Falkenb. L.
Heterosiphonia dubia (Suhr) Falkenb. S (Wynne, 1986).
Heterosiphonia sp. TB.
Hildenbrandia rubra (Sommerfelt) Menegh. EB, L, RP, S, TB.
Hymenena venosa (L.) Kylin EB, L.
Hypnea ceramioides Kütz. RP (Penrith & Kensley, 1970*b*).
Hypnea eckloni Suhr see *Hypnea musciformis* note in Delf & Michell (1921).
Hypnea musciformis (Wulf.) Lamouroux S (Wynne, 1986), WB (Delf & Michell, 1921, as *Hypnea eckloni*).
Hypnea spicifera (Suhr) Harvey AB, KR (Kensley & Penrith, 1980), L, RP (Penrith & Kensley, 1970*b*)*.
Hypnea (?)tenuis Kylin KR.
Hypnea spp. KR, L, MB, RP, S, TC.
Hypoglossum sp. TC.
Iridaea capensis J. Agardh CF, D, EB, G, HL, L (Penrith & Kensley, 1970*a*)*; MB, S (Wynne, 1986, as *Iridaea capensis*)*, TC.
Iridaea elongata Suhr WB (Delf & Michell, 1921).
Kallymenia schizophylla J. Agardh L, S (Wynne, 1986)*, TC.
?*Kallymenia* sp. L.
Lithophyllum sp. RP.
Lithothamnion sp. D, L (Penrith & Kensley, 1970*a*), RP (Penrith & Kensley, 1970*b*).
Lomentaria patens Kütz. WB (Delf & Michell, 1921).
Microcladia sp. TC.
Neuroglossum binderianum Kütz. EB, L.
Nitophyllum fissum (Grev.) J. Agardh L (Pilger, 1908). See *Hymenena venosa.*
Nothogenia erinacea (Turner) Parkinson CF, L, MB, RP (Penrith & Kensley, 1970*b* as *Chaetangium erinaceum*), L (Pilger, 1908 as *Chaetangium ornatum*), S (Wynne, 1986)*, TB, WB (Delf & Michell, 1921, as *Chaetangium ornatum*).
Nothogenia magnifica (Pilger) J.Price S (Pilger, 1908; Price et al., 1986).
Nothogenia ovalis (Suhr) Parkinson G, L (Penrith & Kensley, 1970a as *Chaetangium ovale*)*, MB.

Ophidocladus simpliciusculus (P. Crouan & H. Crouan ex J. Agardh) Falkenb. S (Wynne, 1986).
Orcasia pulla Simons see *Strebloclada camptoclada*.
Pachymenia carnosa (J. Agardh) J. Agardh AF (Kensley & Penrith, 1980), CF (Kensley & Penrith, 1980)*, EB, KR (Kensley & Penrith, 1980), L, MB, S (Wynne, 1986)*, TC.
Phyllymenia belangeri (Bory) Setch.& N.Gardner CF, L, S (Wynne, 1986)*, TB, TC.
Platysiphonia miniata (J. Agardh) Børgesen EB, L, MB, RP, TB.
Platysiphonia sp. MB.
Pleonosporium harveyanum (J. Agardh) De Toni L.
Plocamium corallorhiza (Turner) Harvey K.
Plocamium cornutum (Turner) Harvey D, EB, L (Pilger, 1908)*, S (Wynne, 1986)*.
Plocamium glomeratum J. Agardh S (Wynne, 1986)*.
Plocamium rigidum Bory L, RP, S (Wynne, 1986)*, TB, TC, MB.
Plocamium suhrii Kütz. RP, TC.
Plocamium vulgare Lamouroux CF, TC, MB.
Polyopes constrictus (Turner) J. Agardh L.
Polysiphonia atrorubescens (Dillwyn) Grev. L.
Polysiphonia urbana Harvey CF, EB, HL, RP, TC, U, WB (Delf & Michell, 1921 as *Polysiphonia corymbifera*).
Polysiphonia virgata (Agardh) Sprengel EB, G, S (Wynne, 1986)*.
Polysiphonia sp. S (Wynne, 1986). *Polysiphonia* spp. L, S, U.
Porphyra capensis Kutz. AF (Kensley & Penrith, 1980), CF (Kensley & Penrith, 1980), D, EB, G, HL, L (Penrith & Kensley, 1970*a*)*, N (Dinter, 1926; John et al., 1979; Piccone, 1884; Pilger, 1908; Schmidt & Gerloff, 1957), RP, S (Wynne, 1986), TC, U. See remarks on p. 159.
Porphyra sp. S.
Pterosiphonia cloiophylla (Agardh) Falkenb. AB, L, RP, S (Wynne, 1986)*, TC.
Rhodophyllis reptans (Suhr) Papenf. S (Wynne, 1986).
Rhodymenia linearis J. Agardh S (Wynne, 1986).
Rhodymenia natalensis Kylin S (Wynne, 1986).
Rhodymenia sp. CF (Kensley & Penrith, 1980), KR.
Schizymenia obovata (J. Agardh) J. Agardh L, S (Wynne, 1986)*.
Schottera nicaeensis (Lamouroux ex Duby) Guiry & Hollenberg S (Wynne, 1986).
Strebloclada camptoclada (Mont.) Falkenb. AF (Kensley & Penrith, 1980 as *Orcasia pulla*), CF (Kensley & Penrith, 1980 as *Orcasia pulla*), KR (Kensley & Penrith, 1980 as *Orcasia pulla*), MB, RP, S (Wynne, 1986), TC, TS, U.
Strebloclada corymbifera (Agardh) Kylin RP, S (Wynne, 1986).
Strebloclada fasciculifera (Kutz.) Falkenb. RP, TC.
Stylonema alsidii (Zanard.) Drew S (Wynne, 1986).
Suhria vittata (L.) J. Agardh EB, L (Pilger, 1908)*, MB, S (Wynne, 1986)*.
Tayloriella tenebrosa (Harvey) Kylin MB, RP, S, TB, TS.
Tayloriella virgata (Agardh) Papenf. see *Polysiphonia virgata*.
Tayloriella sp. RP, TC.
Trematocarpus flabellatus (J. Agardh) De Toni EB, L, N (Price et al., 1986).

CYANOPHYCEAE

Lyngbya sp. L (Penrith & Kensley, 1970*a*).

Acknowledgments. The authors are grateful to the State Department of Agriculture of the Union of South Africa (now the Republic of South Africa) for providing a four-wheel-drive vehicle and all its fuel and maintenance needs. They also thank the Administration of Consolidated Diamond Mines for permission to visit Elizabeth Bay. The University of Cape Town and the Council for Scientific and Industrial Research helped by funding some of the travelling expenses of the party.

We are indebted to Miss Judith Graves for her participation in the original field excursion of 1957, and to Dr D. M. John and Mr J. H. Price of The Natural History Museum, London, who read the paper critically and provided additional information and advice, and to the Photographic Unit of the museum for providing black and white prints from the colour slides made by one of us (G.W.L.).

REFERENCES

Anon. 1963. *Africa pilot* **2**. London.
Anon. 1964. *Handbuch der Westküste Afrikas II. Teil von Calabar River bis Cape Hangklip*. Hamburg.
Barton, E. S. 1893. A provisional list of the marine algae of the Cape of Good Hope. *J. Bot., Lond.* **31**: 53–56, 81–84, 110–114, 138–144, 171–177, 202–210.
—— 1896. Cape algae. *J. Bot. Lond.* **34**: 193–198.
Bolton, J. J. 1986. Marine phytogeography of the Benguela upwelling region on the west coast of southern Africa: a temperature dependent approach. *Botanica mar.* **29**: 251–256.
—— **& Anderson, R. J.** 1988. Gradient analysis of seaweed communities around the southern tip of Africa. *Third Internat. Phycol. Congr., Monash Univ., 1988* Abstr.: 5.
Branch, M. 1974. Limiting factors for the gametes of three South African laminariales. *Investl. Rep. Sea Fish. Brch. S. Afr.* **104**: 1–38.
Briggs, J. C., 1974. *Marine zoogeography*. New York.
Bright, K. M. F. 1938. The South African intertidal zone and its relation to ocean currents. III.—An area on the northern part of the west coast. *Trans. R. Soc. S. Afr.* **26**: 67–88.
Brown, A. C. & Jarman, N.. 1978. Coastal marine habitats. *In* M.J.A. Werger (Ed.), *Biogeography and ecology of southern Africa* **2**: 1239–1277. [Monographiae Biologicae **31**]. The Hague.
Delf, E. M. & Michell, M. R. 1921. The Tyson collection of marine algae. *Ann. Bolus Herb.* **3**: 89–119.
De Toni, G. B. 1895. Sylloge algarum omnium hucusque cognitarum III. *Sylloge Fucoidearum*. Padova.
Dinter, K. 1919–1928. Index, der aus Deutsch-Südwestafrika bis zum Jahre, 1917 bekannt gewordenen Pflanzenarten. *Reprium Spec. nov. Regni veg.* **16**: 239–244; **17**: 303–311; **18**: 13–16, 248–256, 423–444; **19**: 315–320; **22**: 108–112, 375–383; **23**: 130–137, 363–371; **24**: 302–304.
Ekman, S. 1953. *Zoogeography of the sea*. London.
Feldmann, J. 1946. La flore marine des Îles Atlantides. *Mém. Soc. Biogéogr.* **8**: 395–435.
Foslie, M. 1893. Ueber eine neue *Laminaria (Laminaria schinzii)* aus Westafrika. *Bull. Herb. Boissier* **1**: 91–94.
Hedgpeth, J. W. 1957. Marine biogeography. *Geol. Soc. Am. Memoir.* **67**: 359–382.
Hoek, C van den 1984. World-wide latitudinal and longitudinal distribution patterns and their possible causes as illustrated by the distribution of Rhodophycean genera. *Helgoländer wiss. Meeresunters.* **38**: 227–257.
Hommersand, M. H., 1986. The biogeography of the South African marine red algae: a model. *Botanica mar.* **29**: 257–270.
Isaac, W. E. 1937*a*. South African coastal waters in relation to coastal currents. *Geographical Rev.* **27**: 651–664.
—— 1937*b*. Studies of South African seaweed vegetation. 1.—West coast from Lamberts Bay to the Cape of Good Hope. *Trans. R. Soc. S. Afr.* **25**: 115–151.
—— 1949. Studies of South African seaweed vegetation. II.—South coast: Rooi Els to Gansbaai, with special reference to Gansbaai. *Trans. R. Soc. S. Afr.* **32**: 125–160.
—— 1956. The ecology of *Gracilaria confervoides* (L.) Grev. in South Africa with special reference to its ecology in the Saldanha-Langebaan lagoon. *Proc.Int. Seaweed Symp.* (Trondheim, 1955) **2**: 173–185. London.
—— 1957. The distribution, ecology and taxonomy of *Porphyra* on South African coasts. *Proc. Linn. Soc. Lond.* **168**: 61–65.
—— **& Hewitt, F.** 1953. The morphology, geographical distribution and ecology of *Hypnea spicifera* (Suhr) Harv. *Jl S. Afr. Bot.* **19**: 73–84.
John, D. M. 1986. Littoral and sublittoral vegetation. *In* G. W. Lawson (Ed.) *Plant ecology in West Africa: systems and processes*: 215–246. Chichester.
—— **& Lawson, G. W.** 1990. Littoral ecosystems of tropical West Africa. *In* A. C. Mathieson & P. H. Nienhuis (Eds), *Intertidal and littoral ecosystems*. Elsevier Series *Ecosystems of the World* **24** (in press).

—— —— **& Price, J. H.** 1981. Preliminary results from a recent survey of the marine algal flora of Angola (southwestern Africa). *Proc. Int. Seaweed Symp.* (Bangor, 1974) **8**: 367–371. Menai Bridge.
—— **Price, J. H., Maggs, C. A. & Lawson, G. W.** 1979. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. III. Rhodophyta (Bangiophyceae). *Bull. Br. Mus. nat. Hist.* (Bot.) **7**: 69–82.
Kensley, B. & Penrith, M.-L. 1973. The constitution of the intertidal fauna of rocky shores of Moçamedes, southern Angola. *Cimbebasia* A, **2**: 113–123.
—— —— 1980. The constitution of the fauna of rocky intertidal shores of South West Africa. Part III. The north coast from False Cape Frio to the Kunene River. *Cimbebasia* A, **5**: 201–214.
Knox, G. A. 1960. Littoral ecology and biogeography of the southern oceans. *Proc. R. Soc.* B. **152**: 577–624.
Kühnemann, O., 1972. Bosquejo fitogeográfico de la vegetación marina del litoral argentino. *Physis* **31**: 117–142.
Lawson, G. W. 1978. The distribution of seaweed floras in the tropical and subtropical Atlantic Ocean: a quantitative approach. *Bot. J. Linn. Soc.* **76**: 177–193.
—— 1988. Seaweed distribution patterns as revealed by ordination with reference to the Atlantic and southern oceans. *Helgoländer wiss. Meeresunters.* **42**: 187–197.
—— **John, D. M. & Price, J. H.** 1975. The marine algal flora of Angola: its distribution and affinities. *Bot. J. Linn. Soc.* **70**: 307–324.
—— **& Price, J. H.** 1969. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. I. Chlorophyta and Xanthophyta. *Bot. J. Linn. Soc.* **62**: 279–346.
Lewis, J. R. 1961. The littoral zone on rocky shores—a biological or physical entity? *Oikos* **12**: 280–301.
Lüning, K. 1985. *Meeresbotanik*. Stuttgart.
McLachlan, A. 1985. The ecology of two sandy beaches near Walvis Bay. *Madoqua* **14**: 155–163.
Michanek, G. 1971. A preliminary appraisal of world seaweed resources. *Fish Circ.* **128**. Roma.
—— 1975. Seaweed resources of the ocean. *Fish. Tech. Pap.* **138**. Roma.
—— 1979. Phytogeographical provinces and seaweed distribution. *Botanica mar.* **22**: 375–391.
Papenfuss, G. F. 1968. Notes on South African marine algae V. *Jl S. Afr. Bot.* **34**: 267–287.
Penrith, M.-L. & Kensley, B. F. 1970*a*. The constitution of the intertidal fauna of rocky shores of South West Africa. Part 1. Lüderitzbucht. *Cimbebasia* A, **1**: 191–239.
—— —— 1970*b*. The constitution of the fauna of rocky intertidal shores of South West Africa. Part II Rocky Point. *Cimbebasia* A, **1**: 243–268.
Piccone, A. 1884. *Crociera del Corsaro alle isole Madera e Canarie del Capitano Enrico d'Albertis. Alghe*. Genova.
Pilger, R. 1908. Kleinere Beiträge zur Kenntnis der Meeresalgen 1. *Hedwigia* **48**: 178–183.
Pollock, D. E. & Beyers, C. J. de B. 1981. Environment, distribution and growth rates of west coast rock-lobster *Jasus lalandii* (H. Milne Edwards). *Trans. R. Soc. S. Afr.* **44**: 379–400.
Post, E. 1963. Zur Verbreitung und Ökologie der *Bostrychia-Caloglossa* Assoziation. *Int. Rev. ges. Hydrobiol.* **48**: 47–152.
Price, J. H., John. D. M. & Lawson, G. W. 1978. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment.II. Phaeophyta. *Bull. Br. Mus. nat. Hist.* (Bot.) **6**: 87–182.
—— —— —— 1986. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. IV. Rhodophyta (Florideae) 1. Genera A–F. *Bull. Br. Mus. nat. Hist.* (Bot.) **15**: 1–122.
—— —— —— 1988. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. IV. Rhodophyta (Florideae) 2. Genera G. *Bull. Br. Mus. nat. Hist.* (Bot.) **18**: 195–273.
Rotmann, K. W. G., 1987. The collection, utilization and potential farming of red seaweeds in Namibia. *Hydrobiologia* **151/152**: 301–305.
Round, F. E. 1981. *The ecology of algae*. Cambridge.
Searles, R. B. 1968. Morphological studies of red algae of the order Gigartinales. *Univ. Calif. Pubs. Bot.* **43**.
Schmidt, O. C. 1923. Beiträge zur Kenntnis der Gattung *Codium* Stackh. *Bibliotheca Bot.* **91**: 1–67.
—— **& Gerloff, J.** 1957. Die marine vegetation Afrikas in ihren Grundzügen darstellt. *Willdenowia* **1**: 709–756.
Seagrief, S. C. 1984. A catalogue of South African green, brown and red algae. *Mem. Bot. Surv. S. Afr.* **47**.
—— **& Troughton, S. C.** 1973. A guide to the literature on South African marine algae. *Jl S. Afr. Bot.* **39**: 95–109.
Shannon, L. V., Agenbag, J. J. & Buys, M. E. L. 1987. Large and mesoscale features of the Angola—Benguela front. *In* A. I. L. Payne, J. A. Gulland & K. H. Brink (Eds) *The Benguela and Comparable Ecosystems. S. Afr. J. mar. Sci.* **5**: 11–34.
—— **Nelson, G. & Jury, M. R.** 1981. Hydrological and meteorological aspects of upwelling in the south Benguela Current. *In* F. A. Richards (Ed.) *Coastal and estuarine sciences* **1**: 146–159.
Silva, P. C. 1959. The genus *Codium* (Chlorophyta) in South Africa. *Jl S. Afr. Bot.* **25**: 103–165.
—— 1960. *Codium* (Chlorophyta) in the tropical western Atlantic. *Nova Hedwigia* **1**: 497–536.
Simons, R. H. 1964. Species of *Plocamium* on the South African coast. *Bothalia* **9**: 153–168.
—— 1966. The genus *Ceramium* in South Africa. *Bothalia* **9**: 153–168.
—— 1968. Notes on *Ceramium planum* Kützing, a red seaweed from South Africa. *Jl S. Afr. Bot.* **34**: 127–133.
—— 1970. Marine algae from South Africa 1. Six new species from the inter- and infra-tidal zones. *Investl. Rep. Div. Sea Fish. Rep. S. Afr.* **88**: 1–13.
—— 1974. Algae (including diatoms and seaweeds) *In* J. H. Day, N. A. H. Millard & M. L. Penrith (Eds), *A guide to the marine life on South African shores*. 2nd ed.: 239–261. Cape Town.
—— 1983. The genus *Trematocarpus* (Sarcodiaceae, Rhodophyta) in southern Africa and the exclusion of *Sphaerococcus (Chondrus) scutellatus*. *Bothalia* **14**: 803–808.
—— **& Hewitt, F. E.** 1977. Marine algae from southern Africa 2. Morphology and taxonomy of five foliaceous Floridiophyceae (Rhodophyta). *Investl. Rep. Div. Sea Fish. S. Afr.* **110**: 1–46.
Stephenson, T. A. 1939. The constitution of the intertidal fauna and flora of South Africa. Part 1. *J. Linn. Soc.* (Zool.) **40**: 478–536.
—— 1944. The constitution of the intertidal fauna and flora of South Africa. Part II. *Ann. Natal Mus.* **10**: 261–358.
—— 1948. The constitutiobn of the intertidal fauna and flora of South Africa. Part III. *Ann. Natal Mus.* **11**: 207–324.
—— **& Stephenson, A.** 1972. *Life between tidemarks on rocky shores*. San Francisco.
—— —— **& Day, J. H.** 1940. The South African intertidal zone and its relation to ocean currents. VIII Lambert's Bay and the west coast. *Ann. Natal Mus.* **9**: 345–377.
Sverdrup, H. U., Johnson, M. W. & Flemming, R. H. 1942. *The oceans*. New York.
Wynne, M. J. 1986. Report on a collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia* **43**: 311–355.

Bull. Br. Mus. nat. Hist. (Bot.) **20**(2) 169–192 Issued 20 December 1990

The infrageneric classification of *Gentiana* (Gentianaceae)

ISRN 86487

TING-NUNG HO and SHANG-WU LIU

Northwest Plateau Institute of Biology, Academia Sinica, Xining, Qinghai, China

CONTENTS

Generic circumscription and status 170
Key to the genera in subtribe Gentianinae 170
Infrageneric classification 171
Taxonomic characters 172
Systematic treatment 178
Gentiana L. 178
Key to the sections 178
Keys to the series 179
Classification 179
I. Sect. *Otophora* Kusn. 179
1. Ser. *Otophorae* Marquand 180
2. Ser. *Decoratae* Marquand 180
II. Sect. *Cruciata* Gaudin 180
III. Sect. *Monopodiae* (H. Smith) T.N.Ho 180
1. Ser. *Monanthae* (H. Smith) T.N.Ho 180
2. Ser. *Verticillatae* (Marquand) T.N.Ho 180
3. Ser. *Ornatae* (Marquand) T.N.Ho 180
4. Ser. *Apteroideae* (H. Smith) T.N.Ho 180
IV. Sect. *Frigida* Kusn. 181
V. Sect. *Gentiana* 181
VI. Sect. *Pneumonanthe* (Gled.) Gaudin 181
VII. Sect. *Phyllocalyx* T.N.Ho 181
VIII. Sect. *Calathianae* Froelich 181
IX. Sect. *Ciminalis* (Adans.) Dumort. 181
X. Sect. *Isomeria* Kusn. 181
1. Ser. *Sikkimenses* (Marquand) T.N.Ho 182
2. Ser. *Depressae* (H. Smith) T.N.Ho 182
3. Ser. *Stragulatae* T.N.Ho 182
4. Ser. *Uniflorae* (Marquand) T.N.Ho 182
XI. Sect. *Microsperma* T.N.Ho 182
1. Ser. *Suborbisepalae* (Marquand) T.N.Ho 182
2. Ser. *Tetramerae* (Marquand) T.N.Ho 182
3. Ser. *Annuae* (Marquand) T.N.Ho 182
XII. Sect. *Stenogyne* Franchet 182
XIII. Sect. *Dolichocarpa* T.N.Ho 182
XIV. Sect. *Chondrophyllae* Bunge 182
1. Ser. *Fimbriatae* Marquand 183
2. Ser. *Rubicundae* Marquand 183
3. Ser. *Linearifoliae* Marquand 183
4. Ser. *Orbiculatae* Marquand 183
5. Ser. *Humiles* Marquand 183
6. Ser. *Capitatae* T.N.Ho 183
7. Ser. *Fastigiatae* T.N.Ho 183
8. Ser. *Napuliferae* T.N.Ho 183
9. Ser. *Coriaceae* T.N.Ho 183
10. Ser. *Piasezkianae* T.N.Ho 183
11. Ser. *Grandiflorae* Grossh. ex T.N.Ho 184
XV. Sect. *Fimbricorona* T.N.Ho 184
Geographical distribution 184
Study materials 191
References 191

Synopsis. An infrageneric classification of the genus *Gentiana* L. is presented. The genus is divided into 15 sections, of which five are subdivided into series, including 361 species. Two series, *Coriaceae* T.N. Ho and *Grandiflorae* Grossh. ex T.N. Ho, are described as new, and the new combination, ser. *Monanthae* (H. Smith) T.N. Ho, is made. *Fimbricorona* T.N. Ho is proposed as a new name for sect. *Eurythalia* (Borkh.) Griseb. Keys are given to the genera in subtribe Gentianinae and the sections and series of *Gentiana*. The history of the infrageneric classification of *Gentiana*, the characters used in infrageneric classification, and the geographical distribution of the genus are discussed.

GENERIC CIRCUMSCRIPTION AND STATUS

The name *Gentiana* in its modern sense is generally accredited to Tournefort (1700). His name was taken up by Linnaeus in *Genera plantarum* (1737) and *Species plantarum* (1753).

Gentiana sensu lato, as traditionally circumscribed, is a very heterogeneous assemblage of morphologically diverse groups, including *Tripterospermum, Crawfurdia, Megacodon,* and *Gentianella* sensu lato. *Gentianella* sensu lato further consists of *Gentianella* sensu stricto, *Comastoma, Gentianopsis,* and *Pterygocalyx*. *Gentiana* is circumscribed in the present paper in the strict sense, as equivalent to subgenus *Eugentiana* Kusn. This interpretation has been accepted widely by most 20th century authors on Gentianaceae, e.g. Smith (1936, 1965), Tutin (1972), Czerepanov (1973), Pringle (1977, 1978, 1979). It is narrower than *Gentiana* sensu lato mentioned above, but much broader than *Gentiana* as defined by Holub (1973) and Löve & Löve (1975) who restricted *Gentiana* to the five European species treated by Tutin (1972) as sect. *Gentiana*.

According to Gilg's comprehensive survey of the family (1895), *Gentiana* is included in subfamily Gentianoideae, tribe Gentianeae, subtribe Gentianinae. In subtribe Gentianinae, it is more closely related to *Crawfurdia, Tripterospermum,* and *Megacodon* than to *Gentianella, Comastoma, Gentianopsis, Lomatogonium, Lomatogoniopsis, Swertia,* and *Halenia*. It seems that these genera can be split into two evolutionary groups—the *Gentiana* group and the *Gentianella* group. The two groups can be clearly distinguished on the basis of the position of the floral glands: the *Gentiana* group (*Gentiana, Crawfurdia, Tripterospermum,* and *Megacodon*) has glands at the base of the ovary, while the *Gentianella* group (*Gentianella, Comastoma, Gentianopsis, Lomatogonium, Lomatogoniopsis, Swertia,* and *Halenia*) has glands in foveae or spurs borne on the surface of the corolla (epipetalous glands). In addition, the corolla bears plicae or folds between the lobes in the *Gentiana* group (except in *Gentiana lutea* L. and *Megacodon*), each lobe has 3 primary vascular bundles, the calyx has a continuous intracalycular membrane (except in *Gentiana* sect. *Chondrophyllae* and sect. *Calathianae* which have obsolete membranes), and calcium oxalate crystals have been reported in the leaf mesophyll (except in sect. *Calathianae*). In the *Gentianella* group, there are no plicae or folds between the corolla-lobes and there is no continuous intracalycular membrane, the corolla-lobes have 5–9 vascular bundles, and calcium oxalate crystals have not been found in the leaf mesophyll. *Crawfurdia* and *Tripterospermum* are further characterized by their climbing habit and by the calyx having 10 vascular bundles in the former and 5 in the latter, and differ distinctly from *Gentiana* in these characters.

Chromosome data have contributed little towards resolving the problem of generic delimitation in the Gentianinae. From previously reported chromosome data, we know that the majority of perennial species of *Gentiana* are x = 6 or 13, 2n = 12 or 26, less often x = 5, 7, 9, or 11, 2n = 10, 14, 18, 20, 22, 24, 30, 36, 40, 44, 48 or 52. The majority of annuals are x = 5, 2n = 10, less often x = 13 or 19, 2n = 26 or 38. However, in *Gentianella,* the chromosome number x = 9, 2n = 36 is the commonest and most widespread one. The base number is x = 9 or 13 in *Swertia*. *Halenia* has a base number of 11, 2n = 22. The diploid *Comastoma* has a base number of 5 in common with *Lomatogonium*. *Gentianopsis* has two series, x = 11 or 13, 2n = 44 or 78. However, in these genera, sometimes more than one series of numbers may exist in the same genus, even in the same section or within a group with very similar morphological features. For example, *Gentiana frigida* Haenke and *G. froelichii* Jan ex Reichenb., both endemic to Europe and belonging to sect. *Frigida*, have different chromosome base numbers, x = 6 and x = 7 respectively. Only about half the genera of Gentianaceae have been investigated cytologically, and only selected species rather than whole genera. Further study is clearly necessary.

Most pollen grains in Gentianinae are 3-colporate, less frequently 3-colpate (-colporoidate), or occasionally 4-colporate (-colporoidate). The size of the pollen grains (length of polar axis) ranges from 15 μm to 65 μm. The shape varies from peroblate to perprolate. The sexine patterns can be classified into striate, striato-reticulate, reticulate, spinuliferous and smooth, and the diversity seems to follow the generic or sectional classification. Most species of *Gentiana* have striate sexine, rarely striato-reticulate (sect. *Chondrophyllae* and sect. *Calathianae*). The ora usually have lateral extensions. *Gentianopsis* has typically reticulate, heterobrochate pollen grains. The ora are distinctly delimited or are visible only in lateral view. *Swertia* has heterogeneous sexine features, i.e. striate, striato-reticulate, reticulate, spinuliferous or smooth. *Halenia* has pollen grains which are finely reticulate. *Lomatogonium* is characterized by the presence of 'islands', and by the sexine distinctly overlapping the ora. Its sexine patterns are striate to striato-reticulate or the tectum is provided with spinules or is punctate. *Comastoma* has pollen grains resembling those of *Lomatogonium* p. p. and *Halenia*. The ora are lolongate to lalongate and relatively large with lateral extensions. The sexine patterns are reticulate with the bacula regularly arranged or with the bacula arranged in no particular order, sometimes interconnected by thin connections. It seems likely that further study of the group, using the scanning electron microscope, will provide more taxonomically valuable pollen characters. Nilsson's (1967, 1976) work is an example of the sort of studies that are needed.

Key to the genera in subtribe Gentianinae

1a. Glands in a whorl attached to the base of the ovary:

2a. Corolla with plicae between the lobes (except in *Gentiana*

lutea), divided to less than halfway, the tube much longer than the lobes, rarely divided to more than halfway and the tube shorter than, or equalling, the lobes:

3a. Plants not climbing, with quadrangular, erect or ascending stems ..... **Gentiana**

3b. Plants climbing, with terete, twisted stems:

4a. Vascular bundles in calyx-tube 5; glands conspicuously developed, forming a collar-like disc covering the base of the ovary; stamens asymmetrical, unequal in length, unilaterally and uniformly curved downwards at the apex, the filaments linear or filiform; fruit a capsule or berry ..... **Tripterospermum**

4b. Vascular bundles in calyx-tube 10; glands small, not discoid; stamens symmetrical, equal in length, straight, the filaments thickened below; fruit a capsule ..... **Crawfurdia**

2b. Corolla without plicae between the lobes, divided to more than halfway, the tube shorter than, or equalling, the lobes:

5a. Ovary sub-bilocular, with a lamellate intrusion of the placenta into the locular cavity ..... **Ixanthus**

5b. Ovary unilocular, without a lamellate intrusion of the placenta into the locular cavity:

6a. Stamens inserted on the sinus of the corolla-lobes; capsule twisted above; flowers small ..... **Latouchea**

6b. Stamens inserted on the upper part of the corolla-tube; capsule straight; flowers large ..... **Megacodon**

1b. Glands in foveae, lobes or spurs attached to corolla-tube and alternating with the stamens:

7a. Corolla with spurs at the base of the corolla-tube, rarely spurless; glands prolonged into the spurs ..... **Halenia**

7b. Corolla without spurs; foveae on corolla-tube or on lobes:

8a. Corolla usually tubular, the tube longer than the lobes, less often the tube shorter than, or as long as, the lobes:

9a. Buds large, slightly flattened, 4-angled; pairs of calyx-lobes dissimilar, one longer and narrower than the other; corolla frequently fringed or toothed; seeds angular-papillose ..... **Gentianopsis**

9b. Buds small, not flattened; calyx-lobes usually all similar; corolla not fringed; seeds almost smooth:

10a. Corolla bearing two evascular fimbriate scales at the base of each lobe ..... **Comastoma**

10b. Corolla naked at the throat or bearing vascular fimbriae, the fimbriae united into a single scale extending across the base of each lobe (*Gentianella*):

11a. Stems twining; calyx conspicuously 4-winged; seeds discoid-winged ..... **Pterygocalyx**

11b. Stems erect; calyx unwinged; seeds unwinged:

12a. Corolla imbricate in bud; stamens inserted at, or below, the middle of the corolla-tube; seeds generally numerous per capsule .... **Gentianella**

12b. Corolla valvate in bud; stamens inserted on the sinus between the lobes; seeds few per capsule ..... **Jaeschkea**

8b. Corolla rotate, the tube much shorter than the lobes:

13a. Dioecious, with unisexual flowers; stamens inserted on the sinus between the corolla-lobes ..... **Veratrilla**

13b. Flowers hermaphrodite; stamens inserted on the corolla-tube:

14a. Style present, the stigmas never decurrent; corolla-lobes concolorous ..... **Swertia**

14b. Style absent, the stigmas decurrent along the ventral suture of the ovary; corolla-lobes conspicuously bicolorous, half pale and half dark:

15a. Corolla-lobes bearing conspicuous foveae which are sometimes connate below into a tube, but lobed or lamellate above ..... **Lomatogonium**

15b. Corolla-lobes efoveolate, bearing appendages which are lamellate or galeate, and entire or erose ..... **Lomatogoniopsis**

INFRAGENERIC CLASSIFICATION

Some 40 botanists have studied *Gentiana* intensively since Linnaeus formally established the genus. They not only discovered large numbers of new species, but they have also treated the genus in a wide variety of ways. The taxonomic history has been well documented by Kusnezow (1894) and Gillet (1957), and will therefore not be repeated here in detail. The discussion that follows will just review some of the more important works.

In 1737, when Linnaeus took up Tournefort's *Gentiana* he divided the genus into seven groups. In 1753, he redivided it less successfully into three unnamed sections, describing 23 species, of which the first, *G. lutea* L., has been taken as the type species of *Gentiana* by later authors.

Froelich (1796) was the first to monograph *Gentiana*, and split the genus into four groups of uncertain rank: *Coelanthe, Calathianae, Endotrichae,* and *Crossopetalae,* with 47 species altogether.

Grisebach's monographic study of Gentianaceae is one of the landmarks of work on the family. In *Genera et species Gentianearum* (1838) he divided the genus into seven sections with 125 species. In his treatment of Gentianaceae in De Candolle's *Prodromus* (1845) he redivided it into 15 sections, of which seven (*Asterias, Coelanthe, Pneumonanthe, Tretorrhiza, Chondrophyllae, Thylacites, Cyclostigma,* and *Eurythalia*) belong to *Gentiana* sensu stricto, and increased the number of species to 153.

Kusnezow's monograph of *Gentiana* subgenus *Eugentiana* (1894) and his treatment of *Gentiana* in Engler & Prantl's *Die natürlichen Pflanzenfamilien* (1895) provided the generally accepted basis for the division of *Gentiana* into sections. His subgenus *Eugentiana* corresponds to *Gentiana* sensu stricto as a genus, and was divided into 10 sections (*Coelanthe, Pneumonanthe, Stenogyne, Frigida, Aptera, Chondrophyllae, Otophora, Isomeria, Thylacites,* and *Cyclostigma*), with 162 species.

Marquand published several papers from 1928 to 1937, notably his revision of the Chinese species of *Gentiana* (1937*a*). He usefully subdivided some sections into series, e.g. *Otophora* into ser. *Otophorae* and *Decoratae*; *Frigida* into ser. *Verticillatae, Ornatae, Suborbisepalae, Confertifoliae, Uniflorae, Sikkimenses, Multiflorae,* and *Annuae*; and *Chondrophyllae* into ser. *Pubigerae, Fimbriatae, Orbiculatae, Linearifoliae, Rubicundae,* and *Humiles*; and included 163 species from China (excepting sect. *Dipterospermum* and sect. *Tripterospermum*), of which 34 were new. Grisebach's and Kusnezow's revisions contained only 71 and 162 species respectively of *Gentiana* sensu stricto for the whole world. However, Marquand combined the genera *Crawfurdia* and *Tripterospermum* with *Gentiana* as two additional sections and relegated *Pterygocalyx* to *Gentianella,* which had been excluded from *Gentiana* by him in an earlier paper (1931).

In 1936, Smith raised Hemsley's sect. *Megacodon* to generic rank and almost thirty years later (in 1965) he reinstated *Crawfurdia and Tripterospermum* as two independent genera. In 1961, when Smith studied the *Gentiana*

cachemirica group he subdivided sect. *Frigida* into two subsections: *Monopodiae* and *Sympodiae,* based on differences of branching. This is a very important character in perennial *Gentiana,* which attracted the attention of Serebryakova (1979), who demonstrated the basic models of shoot formation and indicated various evolutionary trends in the genus. This character is further discussed in the present paper.

Ma (1951) segregated sect. *Crossopetalum* from *Gentiana* as a separate genus, *Gentianopsis.*

In a series of papers published between 1967 and 1979, Pringle not only monographed sect. *Pneumonanthe* and sect. *Chondrophyllae* of eastern North America, central America and Mexico, but also made a careful and clear revision of the sectional and subsectional names.

In the present paper, *Gentiana* is split into 15 sections. Five of these are further divided into a number of series. This classification essentially agrees with that of Kusnezow's monograph, but includes several significant changes. It is based on Ho (1985), in which three new sections (*Phyllocalyx, Microsperma,* and *Dolichocarpa*) and five new series (*Stragulatae, Capitatae, Fastigiatae, Napuliferae,* and *Piasezkianae*) were proposed, and subsect. *Monopodiae* was raised to sectional rank. These treatments are supported chiefly by different branching patterns of the stem, various structures of the testa, the presence or absence of a wing on the capsule, features of the calyx, etc. Here we reinstate Grisebach's sect. *Eurythalia,* which has been forgotten for about a century and a half, as a section, but under a new name, *Fimbricorona.* This section is very unusual in *Gentiana* and its fimbriate corona borne at the throat of the corolla reminds one of the genus *Comastoma.* In addition we describe two new series (ser. *Coriaceae* T.N. Ho and ser. *Grandiflorae* Grossh. ex T.N. Ho) and make one new combination, ser. *Monanthae* (H. Smith) T.N. Ho, in sect. *Monopodiae* T.N. Ho. This is a revision of the arrangement in Ho et al. (1988).

TAXONOMIC CHARACTERS

This section deals with those characters used in the infrageneric classification that need explanation.

1. GROWTH HABIT. All species of *Gentiana* are herbs, varying from dwarf plants, only one or a few centimetres high, to tall, robust plants up to 120 cm high (*G. lutea*). About half of the species are annuals belonging to five sections; the other half are perennials and belong to 10 sections.

2. ROOTS. The roots of *Gentiana* are of four types related to the growth habit and the branching of the stems: fibrous roots, fleshy stout tap-roots, fleshy linear-cylindrical roots, and rhizomes or stolons with adventitious roots. The first type is the commonest, the roots being fibrous or even woody. The primary root is rather small but slightly thickened, forming a slender tap-root with few secondary rootlets. This type is found in the annual sections, i.e. *Chondrophyllae, Dolichocarpa, Microsperma, Stenogyne,* and *Fimbricorona.* The second type is confined to sect. *Otophora,* in which the plant has a fleshy, stout cylindrical or fusiform, persistent tap-root and a few smaller secondary rootlets. The third type, in which the plant has several to many fleshy, linear-cylindrical roots arising from the collar, is confined to sect. *Monopodiae* and sect. *Cruciata.* The last type, as the second and third, is always associated with branching of the stem, the plants having rhizomes or stolons with adventitious roots from the nodes. This type is found in the majority of perennial sections, i.e. *Pneumonanthe, Gentiana, Phyllocalyx, Isomeria, Frigida, Ciminalis,* and *Calathianae.*

3. STEM AND BRANCHING. The stem is always erect or ascending, terete, with striae or angles, sometimes having a conspicuous caudex at the base. This is most conspicuous in sect. *Cruciata,* where the plant has a stout caudex sheathed by fibrous old petioles enabling this section to be recognized at a glance. Sect. *Monopodiae* ser. *Monanthae* also has a stout caudex but differs from sect. *Cruciata* in the caudex being sheathed by membranous old petioles. In all the other groups the caudex is indistinct. In the perennial groups, the branching of the stem is a very constant and significant feature, and provides a reliable diagnostic character for the definition and grouping of sections and series. There are two main types as follows (Fig. 1):

A. *Monopodial branching.* The plant consists of a basal rosette with a terminal bud (growing point of the plant axis) sunk in it. This terminal bud has great vitality and can grow continuously, lasting throughout the life of the plant. The flowering stems are produced each year from the axillary buds of the basal leaves of the rosette. This monopodial branching type falls into two subtypes:

a. Perennial flowering stems. The basal rosette is poorly defined, with a few small, linear-triangular leaves. The flowering stems grow continually and can last for several years. This subtype is confined to sect. *Otophora* ser. *Decoratae.*

b. Annual flowering stems. The basal rosette is well-defined, with abundant large leaves. The flowering stems only last for one year. This subtype is confined to sect. *Monopodiae,* sect. *Cruciata,* and sect. *Otophora* ser. *Otophorae.*

B. *Sympodial branching.* In contrast to monopodial branching, in which the growing point is apical and everlasting, the growing point in sympodial branching is lateral and constantly renewed. The plant has rhizomes or stolons, which have nodes, internodes, buds and adventitious roots, but no basal rosette. After a time, growth of the terminal bud slows down and stops, at which the buds on the nodes grow out instead. The flowering shoots are produced annually from buds on the nodes of the rhizomes or stolons, as well as from the apex of the stolons. Sympodial branching is undoubtedly, as has often been explained, more advanced evolutionarily than monopodial branching. Because the terminal bud dies and the lateral buds renew the growth, the plant can produce progressively more and more lateral buds to prodice a more luxuriant form. The sympodial branching of *Gentiana* exhibits two subtypes as follows:

a. Rhizome subtype. The rhizome is usually stout, fleshy and horizontal or ascending, or more rarely vertical under the ground. Adventitious roots and a lateral rosette arise first from a node and then buds in the axils of the outer leaves of the lateral rosette give rise to the flowering stems. This subtype is found in sect. *Frigida,* sect. *Gentiana,* and some species of sect. *Pneumonanthe.* However, most other species of sect. *Pneumonanthe* are somewhat different from this model in that the plants have no rosette and the buds of the nodes give rise to the flowering stems directly.

b. Stolon subtype. This subtype is rather similar to the

Fig. 1 Types of stem branching (diagrammatic). 1–2 monopodial branching, 1. perennial flowering stem: *G. decorata*; 2. annual flowering stem: *G. veitchiorum*. 3–5 sympodial branching: 3–4 rhizome subtype, 3. *G. scabra*; 4. *G. algida*; 5. stolon subtype: *G. depressa* var. *stenophylla*.

rhizome subtype but differs in having overground stolons and runners. The stolons produce runners from the nodes and these runners are ultimately terminated by a lateral rosette with a few small leaves. The central bud of this rosette in time produces the flowering stems. This subtype is the commoner, being found in sect. *Isomeria,* sect. *Phyllocalyx,* sect. *Ciminalis,* and sect. *Calathianae.*

4. LEAVES. The leaves are usually opposite, but in sect. *Monopodiae* ser. *Verticillatae* they are in whorls of 3–8, surrounding the 5–8-merous flowers. The leaves are generally very variable in shape and size so that their taxonomic use is limited, but in sect. *Chondrophyllae* leaf shape may be used for the definition of series and species. Ser. *Linearifoliae,* for example, is notable for its linear leaves.

5. INFLORESCENCE AND FLOWERS. The inflorescence is always a cyme. The cyme may be simple, with 1–3 flowers, and this may be reduced to a single terminal flower, sometimes also with a few flowers in the axils of the uppermost leaves. This is the commonest condition, occurring in almost all the annual sections (except ser. *Capitatae* and some species of sect. *Chondrophyllae)* and in some of the perennial groups. The inflorescence may also be a complex cyme with few to many flowers. The flowers are crowded and either pedicellate in terminal and axillary cymes or sessile in terminal clusters, and sometimes also in few-flowered axillary whorls. This condition is found in sect. *Gentiana,* sect. *Pneumonanthe,* sect. *Cruciata,* etc.

6. CALYX. The calyx-tube is usually entirely tubular, but in sect. *Gentiana* and some species of sect. *Cruciata* and sect. *Frigida* it is split down one side to the middle or to near the base, forming a spathe with small irregular teeth (Fig. 2). The calyx-lobes are mostly triangular, ovate or lanceolate, but in some groups other shapes occur: spathulate or suborbicular and much narrowed at the base in sect. *Isomeria* ser. *Stragulatae* and sect. *Microsperma* ser. *Suborbisepalae;* ovate and contracted at the base in sect. *Chondrophyllae* ser. *Orbiculatae;* filiform in sect. *Chondrophyllae* ser. *Rubicundae*; and subulate with wide bases and acute apices in sect. *Chondrophyllae* ser. *Fimbriatae.* The midribs are distinct, but the degree of development varies considerably. The most prominent midribs are those forming keeled ribs on the outer face which are decurrent into the angles or wings of the calyx-tube. This condition is found in sect. *Stenogyne,* sect. *Dolichocarpa,* sect. *Calathianae,* and sect. *Microsperma* ser. *Tetramerae.*

7. COROLLA. The corolla is important diagnostically and provides a number of characters for the definition of species. It varies in size from 3 mm to 70 mm, although the range is usually relatively restricted and constant within each group. Large corollas are 4–7 cm long, medium-sized ones 2.5–4 cm, and small ones 0.3–2.5 cm. In general, all perennial sections and the annual sect. *Stenogyne* have large or medium-sized corollas, whereas the others (all the annual sections except *Stenogyne*) have small corollas. The corolla is usually 5-lobed, but 6–8-lobed corollas are found in sect. *Monopodiae* ser. *Verticillatae* and in various species of the other sections. In general, the corolla-tube is longer than the lobes, but the reverse condition occurs in sect. *Gentiana* and sect. *Otophora,* in which the corolla is divided to the middle or near the base so that the corolla-tube is as long as, or much shorter than, the lobes. The shape of the corolla varies considerably and the terms used to describe it in this paper are as follows (Fig. 2):

Tubular. The corolla is tubular throughout, with slightly divergent lobes.
Obconical. The corolla-tube is narrowed at the base but gradually widened upwards with patent lobes.
Hypocrateriform. The corolla has a long, narrow, parallel-sided tube and broad flat lobes spreading at right angles to the tube.
Infundibuliform. The corolla-tube is narrowed in the lower part but is gradually widened upwards, with erect-patent lobes.
Campanulate. The corolla has a short, broad, parallel-sided tube and patent lobes.
Urniform. The corolla-tube is very inflated in the middle but contracted below and in the throat, with patent lobes.

These corolla shapes are not entirely clear-cut, and transitional forms, which need not be discussed here, do occur.

The plicae of the corolla apparently exist in all species of *Gentiana* except *G. lutea,* in which their absence is a particularly diagnostic character. There are various degrees of development of the plicae in the different groups (Fig. 2). In sect. *Gentiana* and sect. *Otophora* the poorly developed plicae are very small, asymmetrical and auriculate, whereas in sect. *Chondrophyllae* and sect. *Dolichocarpa* the well-developed plicae are large and symmetrical. These two types represent the two extremes, the plicae of the other sections being more or less intermediate. The margins of the plicae vary from entire, erose, serrate, lacinulate or fimbriate to setose-fimbriate. Sect. *Chondrophyllae* ser. *Fimbriatae* is notable in that the corolla has fimbriate plicae.

8. STAMENS. The stamens are equal in number to the corolla-lobes and alternate with them. They are generally 5 in number, but in some species of sect. *Monopodiae* ser. *Verticillatae* (where the flowers are 6–8-merous and the leaves are in whorls of 6–8) they are 6–8. The great majority of species have uniform stamens with more or less winged filaments and free anthers, but in some species of sect. *Pneumonanthe* and sect. *Gentiana* the anthers are contiguous.

9. PISTIL. The ovary, which is markedly uniform in general structure, varies mainly in size. It is usually oblong or elliptical and narrowed into the style, or the style may be absent. The style is shortly cylindrical to narrowly linear, much shorter than the ovary in most species, but in sect. *Stenogyne* and a few other species (e.g. *G. filistyla* Balf. f. & Forrest ex Marquand, *G. tubiflora* (G. Don) Wallich ex Griseb., and *G. vernayi* Marquand) the style and stigmas are very long and filiform, equalling, or only slightly shorter than, the elongate ovary. The stigma-lobes in most sections are uniformly oblong or linear and are free and recurved. However, in a few sections they depart from this norm and the stigma-lobes are expanded and rounded, and either fimbriate on the surface and contiguous into a small disc or infundibuliform structure but free after anthesis, or almost smooth and either connate into a small disc or infundibuliform structure and not free after anthesis, or contiguous into a small disc or infundibuliform structure and free after anthesis. The first condition is found in sect. *Ciminalis,* the second in sect. *Calathianae,* and the third in sect. *Phyllocalyx.* These expanded stigmas are diagnostic in *Gentiana* and form the most important character separating the three sections. The gynophore may elongate and become more apparent with age. In some species the pistil is sessile or subsessile, but in others the gynophore may be short in the young flower and elongate

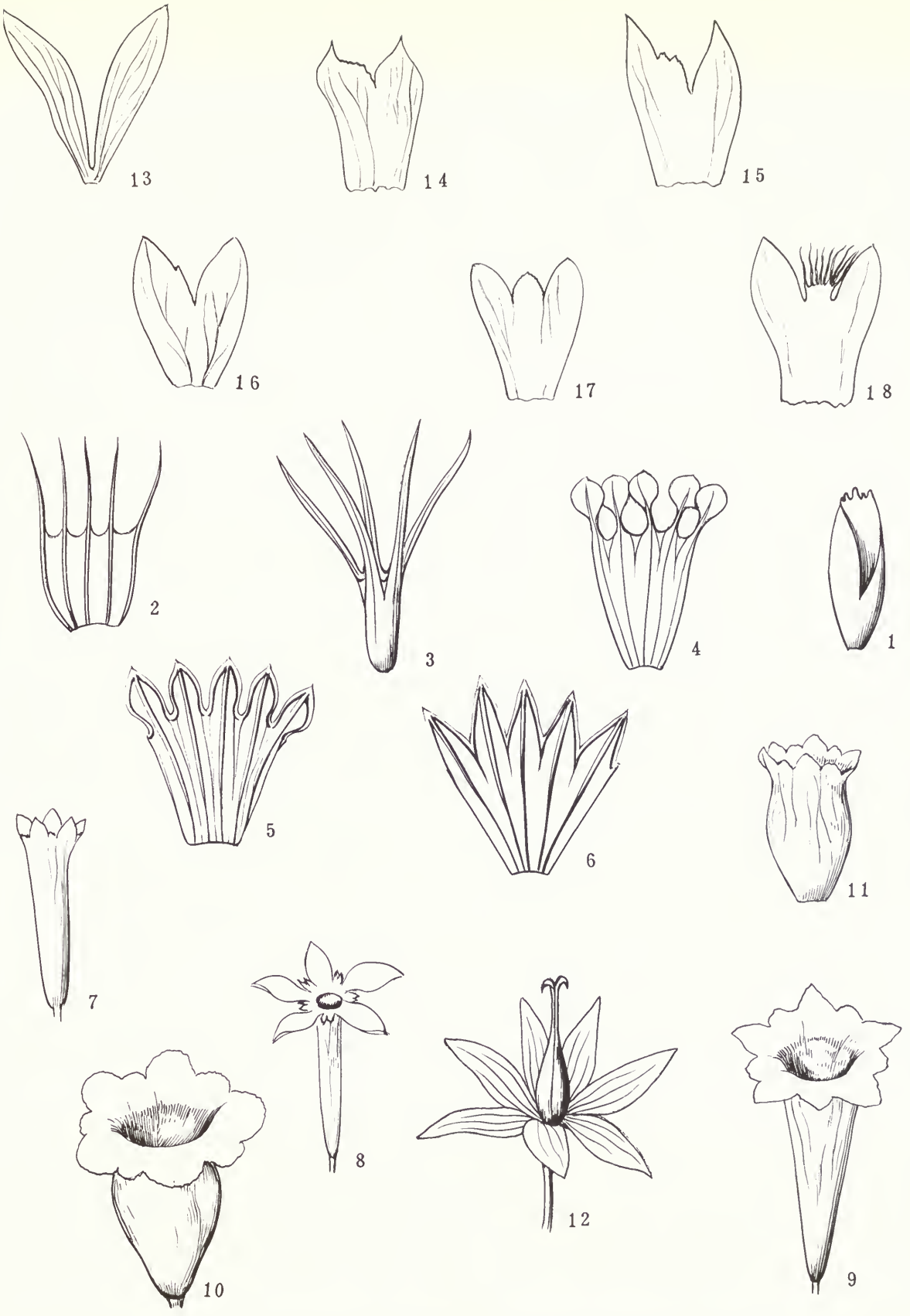

Fig. 2 Calyx, corolla and plica shapes. 1–6 calyx types, 1. calyx-tube split down one side to the lower part to form a spathe with small teeth: *G. straminea*; 2–6 calyx-lobe types, 2. filiform: *G. rubicunda*; 3. linear: *G. dolichocalyx*; 4. suborbicular: *G. tongolensis*; 5. ovate: *G. squarrosa*; 6. triangular: *G. pseudoaquatica*. 7–12 corolla types, 7. tubular: *G. prolata*; 8. hypocrateriform: *G. brachyphylla*; 9. infundibuliform: *G. farreri*; 10. campanulate: *G. alpina*; 11. urniform: *G. urnula*; 12. rotate: *G. lutea*. 13–18 plica types, 13. plica absent: *G. lutea*; 14. truncate: *G. hexaphylla*; 15. oblique: *G. striata*; 16. auriculate: *G. doxiongshanensis*; 17. symmetrical: *G. pseudoaquatica*; 18. fimbriate: *G. panthaica*.

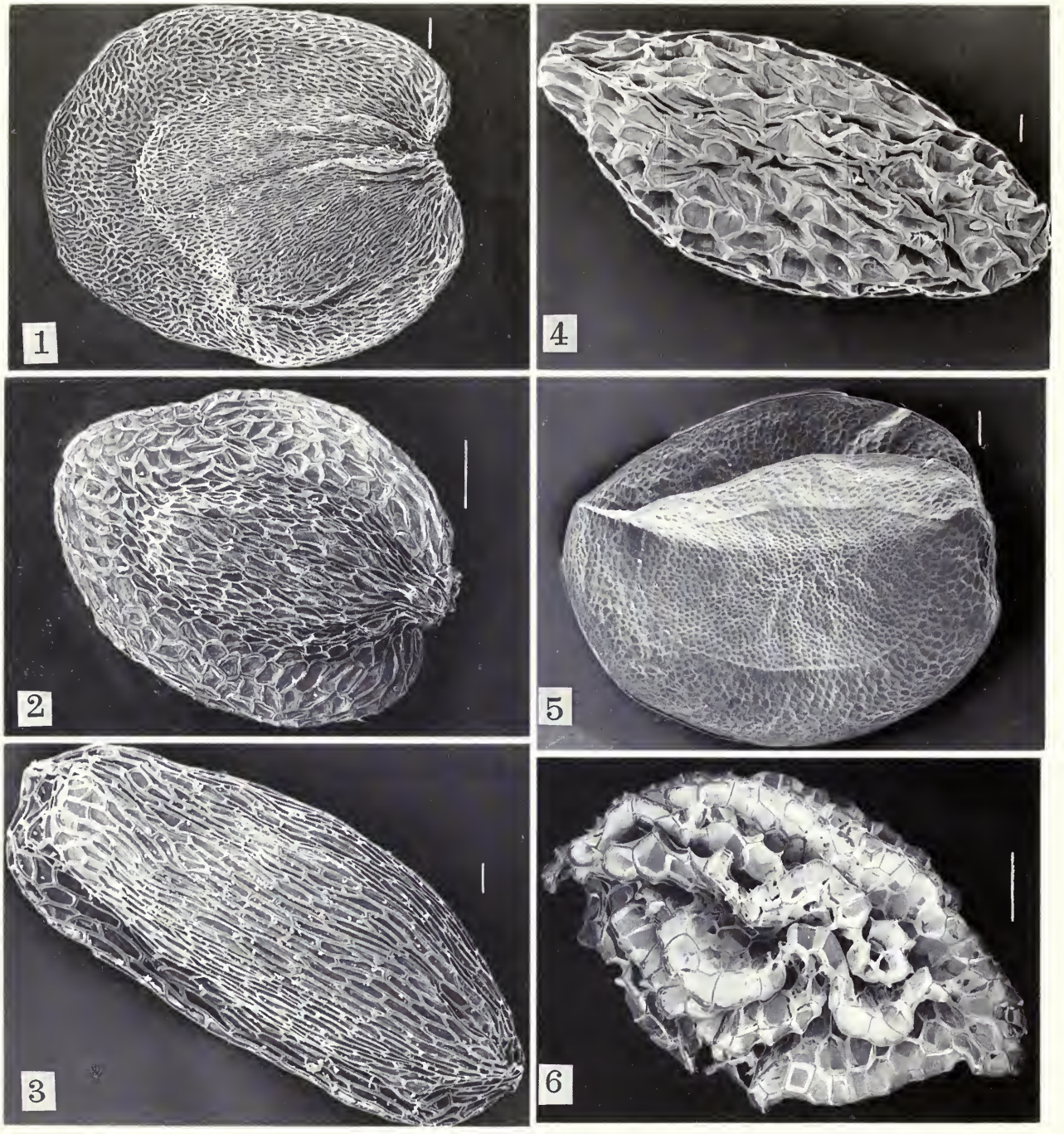

Fig. 3 SEM micrographs of seed types. 1–4 seeds with reticulately thickened testa, winged: 1–2 seeds surrounded by a discoid wing, 1. *G. lutea*; 2. *G. asclepiadea*; 3. seed with wing on one side: *G. pudica*; 4. seed with wing at one end: *G. bavarica*. 5. seed with minutely reticulate testa, triquetrous with the three edges winged: *G. striata*. 6. seed covered with membranous lamellae which form spongy complex pits: *G. algida*. (nos 1, 2, 5, 6, scale = 250 μm; nos 3, 4, scale = 50 μm)

considerably as the capsule matures. It seems that the gynophore is of less taxonomic significance than the style or stigma.

10. CAPSULE. The capsule is usually long and narrow, oblong or cylindrical, and unwinged, but in sect. *Chondrophyllae* and sect. *Fimbricorona* it is short and wide, obovoid or ellipsoid-oblong, strongly compressed, and rounded at the apex with a conspicuous broad wing which is narrowed towards the base.

11. SEEDS. There are six different seed types in the genus (Figs 3–4):

a. The seed has a reticulately thickened testa, with either a discoid wing or with a wing on one side or at one end of the

seed. This type is found in sect. *Gentiana* and sect. *Pneumonanthe,* although some species of sect. *Stenogyne* scarcely differ, their seeds having a minutely reticulate testa and being triquetrous with the three edges winged.

b. The seed varies from almost smooth to distinctly reticulate and is unwinged. This type is the commonest, being found mainly in sect. *Chondrophyllae,* sect. *Dolichocarpa,* sect. *Cruciata,* sect. *Otophora,* and sect. *Calathianae.*

c. The seed is covered with membranous lamellae which form spongy, complex hexagonal pits. This type is confined to sect. *Frigida* and some species of sect. *Isomeria.*

d. The seed is covered with membranous lamellae which form honeycomb-like, simple, shallow, hexagonal pits. This type occurs in sect. *Monopodiae,* sect. *Microsperma,* and some species of sect. *Isomeria.*

e. Like d but the body of the seed is surrounded by a broad wing. This type is found only in sect. *Phyllocalyx.*

f. The seed has a minutely and densely reticulate testa and

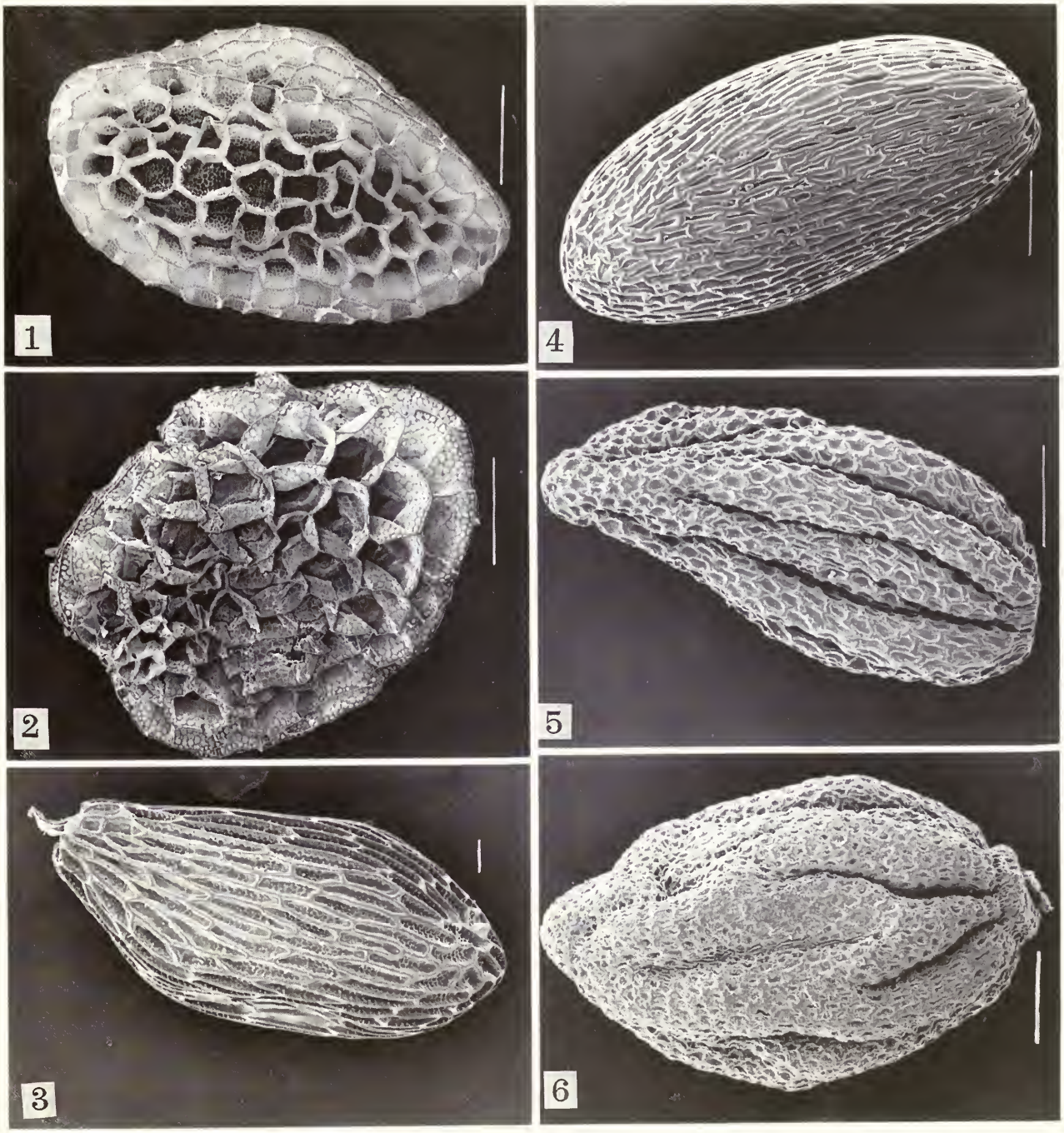

Fig. 4 SEM micrographs of seed types. 1–2 seeds covered with membranous lamellae which form honeycomb-like simple pits, 1. *G. farreri*; 2. *G. tubiflora.* 3–4 seeds minutely reticulate, 3. *G. leucomelaena*; 4. *G. straminea.* 5–6 seeds with minutely and densely reticulate testa, rugose, 5. *G. alpina*; 6. *G. clusii.* (nos 1, 2, 4, 5, 6, scale = 250 μm; no. 3, scale = 50 μm)

is rugose and unwinged. This type is confined to sect. *Ciminalis*.

These seed characters are certainly diagnostically important. However, the different types do sometimes occur in the same section, for instance, a, b, and d all occur in sect. *Stenogyne*, a very natural group in general appearance; c and d both occur in sect. *Isomeria*, a stoloniferous group. Seed characters must therefore not be relied on too heavily, as Kusnezow and Marquand did when delimiting sections. Seed structure is, however, constant within species and may therefore be used for defining species, as well as for the partial delimitation of some sections (e.g. *Cruciata, Chondrophyllae, Microsperma*, etc.).

SYSTEMATIC TREATMENT

Gentiana (Tourn., *Inst. rei herb.*: 80, t. 40 (1700))L., *Gen. pl.*: 69 (1737); *Sp. pl.*: 227 (1753). Type species: *G. lutea* L.

Subgen. *Eugentiana* Kusn. in *Trudy imp. S.-Peterb. Obshch. Estest.* **24**(2): 3 (1894).

Annual or perennial herbs. Roots fibrous with a primary root and secondary rootlets, or slightly fleshy and forming a stout tap-root with secondary rootlets, or several linear-cylindrical roots from the collar. Stem erect or ascending, striate and angled, simple or branched, in perennial species sometimes both flowering stem and vegetative stems present; rhizomes or stolons present or absent. Leaves opposite, rarely verticillate, sometimes forming a rosette at the base of the stem. Cyme simple with 1–3 flowers, or complex with few—many flowers, the flowers pedicellate in terminal and axillary cymes or sessile in terminal clusters or sometimes also in few-flowered axillary whorls; flowers usually 5-merous, rarely 4- or 6–8-merous; calyx-tube with a continuous or undeveloped intracalycular membrane, the lobes triangular, ovate or filiform, with prominent midribs; corolla tubular, infundibuliform, obconical, hypocrateriform, or urniform, very rarely rotate, usually lobed, the tube much shorter than the lobes, or rarely the tube as long as or longer than the lobes, plicate between the lobes (except in *G. lutea* L.); stamens alternate with the corolla-lobes, the filaments more or less winged, the anthers basifixed, free or rarely contiguous; ovary oblong or elliptic; style often short, cylindrical or linear, less often long and filiform, longer or slightly shorter than the ovary, the stigma-lobes usually oblong to linear, free, recurved, rarely expanded and rounded, connate or contiguous into a small disc or infundibuliform structure; glands 5–10, at the base of the ovary, the pistil sessile or with an elongate gynophore. Capsule oblong or cylindrical and unwinged, or obovoid and winged; seeds numerous, small, minutely reticulate, rugose, simply areolate or with complex spongy areolation, winged or unwinged.

DISTRIBUTION. Europe, Asia, America, NW. Africa (Morocco), E. Australia.

Fifteen sections, 361 species.

Key to the sections

1a. Perennials, with thick, slightly fleshy roots, rarely annuals with fibrous roots (*G. nivalis* and *G. utriculosa*); flowers large (4–7 cm long) or medium-sized (2.5–4 cm long); capsule unwinged:

2a. Branching monopodial, the plant with a basal rosette with a terminal bud sunk in it, the flowering stems arising annually from the axillary buds of the rosette leaves:

3a. Corolla usually divided to the middle or below, the tube shorter than, or equalling, the lobes; plicae small, auriculate; plant with a stout, cylindrical or fusiform tap-root ..... I. Sect. **Otophora**

3b. Corolla always divided to less than halfway, the tube much longer than the lobes; plicae large, triangular to truncate; plant with thickened, linear-cylindrical roots from the collar:

4a. Caudex with a fibrous sheath of brown remains of petioles; roots usually contiguous and twisted into a stout, cylindrical mass; seeds minutely but distinctly reticulate ..... II. Sect. **Cruciata**

4b. Caudex without a fibrous sheath of remains of petioles; roots laxly divergent; seeds covered with honeycomb-like, hexagonal, simple, shallow pits .... III. Sect. **Monopodiae**

2b. Branching sympodial, the plant with rhizomes or stolons with nodes, internodes, membranous scales, buds, and adventitious roots, but without a basal rosette with a terminal bud, the flowering stems arising annually from the buds at the nodes or apices of the rhizomes or stolons:

5a. Plants with a stout, slightly fleshy, horizontal or ascending, rarely vertical, underground rhizome, or the rhizome sometimes abbreviated but conspicuous:

6a. Seeds covered with membranous lamellae which form spongy, hexagonal complex pits, unwinged ..... IV. Sect. **Frigida**

6b. Seeds without membranous lamellae, but with a thickened, reticulate testa, winged with either a discoid wing or with a wing on one side or at one end of the seed, or rarely unwinged:

7a. Plants with lateral rosettes which arise from the nodes of the rhizome; flowering stems arising from the axils of the lateral rosette-leaves, without scale-like leaves at the base; corolla lobed to below the middle or to near the base; 5–9-lobed, the plicae very small, auriculate (absent in *G. lutea*) ..... V. Sect. **Gentiana**

7b. Plants without lateral rosettes; flowering stems arising directly from the nodes of the rhizome, usually with scale-like leaves below; corolla lobed to less than halfway, 5-lobed, the plicae large, obliquely truncate or triangular ..... VI. Sect. **Pneumonanthe**

5b. Plants with stolons and runners creeping on the surface:

8a. Stigma-lobes not expanded, linear or oblong, free and recurved ..... X. Sect. **Isomeria**

8b. Stigma-lobes expanded, connate or contiguous into a small disc or infundibuliform structure:

9a. Calyx very small, completely enveloped by the uppermost pair of broad, obovate, obtuse leaves; seeds broadly winged, covered with honeycomb-like, hexagonal, simple, shallow pits ..... VII. Sect. **Phyllocalyx**

9b. Calyx large, not enveloped by the uppermost pair of leaves; seeds unwinged:

10a. Corolla hypocrateriform; calyx-tube prominently angled or winged; stigma-lobes almost smooth, connate into a disc or infundibuliform structure, not free after anthesis; seeds not rugose ..... VIII. Sect. **Calathianae**

10b. Corolla obconical; calyx-tube unwinged; stigma-lobes fimbriate on the surface, contiguous into a disc or infundibuliform structure, but free after anthesis; seeds rugose ..... IX. Sect. **Ciminalis**

1b. Annuals, with fibrous roots; flowers small (0.3–2.5 cm long), or rarely large or medium-sized; rarely perennials with small flowers; capsule winged or unwinged:

11a. Capsule obovoid or ellispoid-oblong, rounded at the apex, conspicuously winged, the wing strong and broad at the apex but gradually narrowed towards the base; basal leaves longer than the cauline; cauline leaves all more or less equal in size:
12a. Corolla naked in the throat ... XIV. Sect. **Chondrophyllae**
12b. Corolla with a corona of multicellular hairs in the throat ... XV. Sect. **Fimbricorona**

11b. Capsule cylindrical to narrowly oblong, obtuse or attenuate at the apex, unwinged; basal leaves small; cauline leaves usually decreasing in size towards the base of the stem:
13a. Seeds covered with honeycomb-like, hexagonal, simple, shallow pits; calyx usually not keeled or winged (if strongly winged, then ser. *Tetramerae*—flowers 4-merous) ... XI. Sect. **Microsperma**
13b. Seeds with minute or thickened reticulation; calyx keeled or winged:
14a. Flowers large or medium-sized; plicae obliquely asymmetrical; style filiform, longer or slightly shorter than the ovary; capsule enclosed in the corolla; seeds usually winged ... XII. Sect. **Stenogyne**
14b. Flowers small; plicae symmetrical; style much shorter than the ovary; capsule exserted from the corolla; seeds usually unwinged ... XIII. Sect. **Dolichocarpa**

Keys to the series

Sect. **Otophora** Kusn.

1a. Basal rosette well-developed, with abundant large leaves; flowering stems annual; cauline leaves few, distant .. 1. Ser. **Otophorae**
1b. Basal rosette poorly developed, with few small leaves; flowering stems perennial; cauline leaves numerous, crowded ... 2. Ser. **Decoratae**

Sect. **Monopodiae** (H. Smith) T.N. Ho

1a. Vegetative axis sometimes prolonged and branched, with several basal rosettes decumbent on the ground; flowers several in a terminal inflorescence ... 4. Ser. **Apteroideae**
1b. Vegetative axis not prolonged, with one basal rosette decumbent on the ground; flowers sometimes solitary and terminal:
2a. Caudex with a brown membranous sheath of old petioles; leaves broad; leaves and calyx-lobes with conspicuous cartilaginous margins ... 1. Ser. **Monanthae**
2b. Caudex without a sheath of old petioles; leaves narrow; leaves and calyx-lobes without cartilaginous margins:
3a. Leaves in whorls of 3–8; flowers 5–8-merous ... 2. Ser. **Verticillatae**
3b. Leaves opposite; flowers 5-merous ... 3. Ser. **Ornatae**

Sect. **Isomeria** Kusn.

1a. Flowers several together in an inflorescence; petioles of upper cauline leaves of flowering stems conspicuously broadened ... 1. Ser. **Sikkimenses**
1b. Flowers typically solitary and terminal; petioles not broadened:
2a. Leaves and calyx-lobes with conspicuous, wide, membranous or cartilaginous margins ... 2. Ser. **Depressae**
2b. Leaves and calyx-lobes without membranous or cartilaginous margins:
3a. Calyx-lobes orbicular-spathulate, narrowed at the base into a tongue ... 3. Ser. **Stragulatae**
3b. Calyx-lobes narrowly elliptical or triangular, not narrowed at the base ... 4. Ser. **Uniflorae**

Sect. **Microsperma** T.N. Ho

1a. Leaves and calyx-lobes spathulate; flowers small; gynoecium and stamens usually exserted from the corolla ... 1. Ser. **Suborbisepalae**
1b. Leaves and calyx-lobes not spathulate; flowers medium-sized; gynoecium and stamens included in the corolla:
2a. Flowers 4-merous; calyx-lobes with strongly keeled midribs which are decurrent below into conspicuous broad wings ... 2. Ser. **Tetramerae**
2b. Flowers 5-merous; calyx unwinged ... 3. Ser. **Annuae**

Sect. **Chondrophyllae** Bunge

1a. Capsule narrowly elliptical, attenuate or obtuse at the apex:
2a. Annuals; flowers 25–36 mm long; calyx-lobes with strongly keeled midribs which are decurrent below into conspicuous wings; corolla hypocrateriform ... 10. Ser. **Piasezkianae**
2b. Perennials; flowers 40–55 mm long; calyx-lobes without keeled midribs; corolla infundibuliform ... 11. Ser. **Grandiflorae**

1b. Capsule obovoid, spathulate or oblong, rounded or truncate at the apex; calyx-lobes not keeled; corolla tubular or infundibuliform:
3a. Annuals:
4a. Calyx-lobes usually very narrow, filiform or filiform-subulate:
5a. Plicae usually fimbriate, rarely dentate; leaves and calyx densely and minutely papillose ... 1. Ser. **Fimbriatae**
5b. Plicae entire or denticulate; leaves and calyx glabrous, smooth ... 2. Ser. **Rubicundae**
4b. Calyx-lobes broad, triangular or lanceolate:
6a. Stems ascending or decumbent, usually branched from the base, without a conspicuous main stem, rarely unbranched:
7a. Cauline leaves mostly long and very narrow, more or less linear or subulate ... 3. Ser. **Linearifoliae**
7b. Cauline leaves short and broad, not linear or subulate:
8a. Calyx-lobes recurved or patent, rarely erect, ovate or orbicular, rarely lanceolate, contracted at the base ... 4. Ser. **Orbiculatae**
8b. Calyx-lobes erect, triangular or lanceolate, not contracted at the base ... 5. Ser. **Humiles**
6b. Stems erect, with a conspicuous main stem, branched or rarely simple:
9a. Stems simple, densely papillose, winged or angled, leafless in the lower half; much branched in the upper half, with abbreviated internodes, numerous leaves and flowering branches, all congested at the apex of the stem into a subcapitate inflorescence . 6. Ser. **Capitatae**
9b. Stems almost glabrous, unwinged, fastigiately branched from the base or the middle, with elongated internodes, the branches lax and more or less corymbosely disposed ... 7. Ser. **Fastigiatae**
3b. Perennials:
10a. Roots rather fleshy; leaves herbaceous ... 8. Ser. **Napuliferae**
10b. Roots fibrous; leaves coriaceous ... 9. Ser. **Coriaceae**

CLASSIFICATION

I. Sect. **Otophora** Kusn. in Engl. & Prantl, *Nat. Pflanzenfam.* **4**(2): 82 (1895). Type species: *G. otophora* Franchet ex F. B. Forbes & Hemsley.

Perennials, with a stout, cylindrical or fusiform, slightly fleshy tap-root; branching monopodial; corolla usually lobed to the middle or below, the tube shorter than, or equalling, the lobes (except in *G. doxiongshanensis* T.N. Ho); plicae very small, auriculate, attached on the right side of each lobe as seen from within; seeds usually minutely reticulate, rarely covered with honeycomb-like, hexagonal, simple, shallow pits.

DISTRIBUTION. C. and E. Himalaya*, E. India (Assam), NE. Burma, SW. China†.

Two series, 12 species.

1. Ser. **Otophorae** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 152 (1937). Type species: *G. otophora* Franchet ex F. B. Forbes & Hemsley.

Plants with well-developed basal rosette; flowering stems annual.

DISTRIBUTION. As for the section.

Eight species.

2. Ser. **Decoratae** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 152 (1937). Type species: *G. decorata* Diels.

Plants with poorly developed basal rosettes; flowering stems perennial.

DISTRIBUTION. As for the section.

Four species.

II. Sect. **Cruciata** Gaudin, *Fl. helv.* **2**: 269 (1828). Type species: *G. cruciata* L.

Sect. *Erythaliae* Bunge in *Nouv. Mém. Soc. imp. Nat. Mosc.* **1**(7): 207 (1829), non (Borkh.) Griseb. (1840). Type species: *G. cruciata* L.

Sect. *Tretorrhiza* Griseb. in Hook., *Fl. bor.-amer.* **2**: 60 (1837). Lectotype species: *G. cruciata* L.

Sect. *Kurroo* C. B. Clarke in *J. Linn. Soc.* (Bot). **14**: 433 (1875). Type species: *G. kurroo* Royle.

Sect. *Aptera* Kusn. in *Trudy imp. S.-Peterb. bot. Sada* **13**: 62 (1893). Lectotype species: *G. biflora* Regel.

Perennials; roots usually contiguous and twisted into a stout, cylindrical structure; branching monopodial; caudex with a brown, fibrous sheath of old petioles; basal rosette well-developed, with large leaves; seeds minutely but distinctly reticulate.

DISTRIBUTION. E., C., and S. Europe, U.S.S.R.—European part; W. Asia (Turkey, Iraq, Iran, Syria, Afghanistan), N. and central part of Asia (Kashmir–Himalayan region, SW. and N. China, U.S.S.R. (Caucasus, C. Asia, W. and E. Siberia, Far East), Mongolia).

Twenty-one species.

III. Sect. **Monopodiae** (H. Smith) T.N.Ho in *Bull. bot. Res. Harbin* **5**(4): 10 (1985).

Subsect. *Monopodiae* H. Smith in *Kew Bull.* **15**(1): 43 (1961). Type species: *G. cephalantha* Franchet ex F. B. Forbes & Hemsley.

Perennials; branching monopodial; seeds covered with honeycomb-like, hexagonal, simple, shallow pits.

DISTRIBUTION. Kashmir–Himalayan region, Burma, NW., SW., C., S., and E. China, Japan, Thailand, Vietnam, Malaya, Indonesia.

Four series, 37 species.

1. Ser. **Monanthae** (H. Smith) T.N. Ho, **comb. nov.**

Sect. *Frigida* ser. *Rosulatae* subser. *Monanthae* H. Smith in *Kew Bull.* **15**(1): 54 (1961). Type species: *G. szechenyii* Kanitz.

Caudex with a brown, membranous sheath of old petioles; leaves broad; leaves and calyx-lobes both with conspicuous cartilaginous margins.

DISTRIBUTION. Kashmir–Himalayan region, SW. and NW. China.

Four species.

2. Ser. **Verticillatae** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 11 (1985).

Kudoa Masam. in *J. trop. Agric.* **2**: 29 (1930). Type species: *G. yakushimensis* Makino.

Sect. *Frigida* ser. *Verticillatae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 158 (1937). Type species: *G. hexaphylla* Maxim. ex Kusn.

Sect. *Kudoa* (Masam.) Satake & Toyok. ex Toyok. in *J. Jap. Bot.* **35**: 202 (1960).

Sect. *Frigida* ser. *Ornatae* subser. *Verticillatae* H. Smith in *Kew Bull.* **15**(1): 54 (1961). Type species: *G. hexaphylla* Maxim. ex Kusn.

Leaves in whorls of 3–8, narrow; flowers solitary, terminal, 5–8-merous.

DISTRIBUTION. China (SW. and NW. regions, except Xinjiang Uygur Zizhiqu, Taiwan), Japan.

Eight species.

3. Ser. **Ornatae** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 11 (1985).

Sect. *Frigida* ser. *Ornatae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 159 (1937). Type species: *G. sino-ornata* Balf. f.

Sect. *Frigida* ser. *Ornatae* subser. *Oppositifoliae* H. Smith in *Kew Bull.* **15**(1): 54 (1961). Type species: *G. sino-ornata* Balf. f.

Leaves opposite, narrow; flowers solitary, terminal, 5-merous.

DISTRIBUTION. C. & E. Himalayan region, Burma, SW. and NW. China.

Sixteen species.

4. Ser. **Apteroideae** (H. Smith) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 11 (1985).

Sect. *Frigida* ser. *Rosulatae* subser. *Apteroideae* H. Smith in *Kew Bull.* **15**(1): 54 (1961). Type species: *G. cephalantha* Franchet ex F. B. Forbes & Hemsley.

Vegetative stems sometimes prolonged and branched, with several basal rosettes decumbent on the ground; flowers several together in infloresences at the apex of the flowering stems.

DISTRIBUTION. Burma, SW., C., E., and S. China, Thailand, Vietnam, Malaya, Indonesia, Sabah.

Nine species.

* Includes Nepal, Sikkim, Bhutan, and S. Tibet.

† The regions of China are—**NW.**: Qinghai, Gansu, Shaanxi, Ningxia-Hui, Xinjiang Uygur Zizhiqu; **N.**: Shanxi, Hebei, Nei Mongol Zizhiqu; **NE.**: Heilongjiang, Jilin, Liaoning; **C.**: Henan, Hubei, Hunan; **E.**: Shandong, Jiangsu, Anhui, Zhejiang, Jiangxi, Fujian, (and Taiwan); **SW.**: Tibet, Yunnan, Guizhou, Sichuan; **S.**: Guangdong, Guangxi-Zhuang.

IV. Sect. **Frigida** Kusn. in *Trudy imp. S.-Peterb. bot. Sada* **13**: 61 (1893). Type species: *G. frigida* Haenke.

Sect. *Frigida* subsect. *Sympodiae* ser. *Algidae* H. Smith in *Kew Bull.* **15**(1): 55 (1961). Type species: *G. algida* Pallas.
Favargera A. & D. Löve in *Bot. Notiser* **125**: 256 (1972). Type species: *F. froelichii* (Kusn.) A. & D. Löve.
Gentianodes A. & D. Löve in *Bot. Notiser* **125**: 256 (1972). Type species: *G. frigida* Haenke.

Perennials; branching sympodial, the plants with a short rhizome, 1–few non-flowering rosettes and 1–few flowering stems; seeds covered with membranous lamellae which form spongy, hexagonal, complex pits.

DISTRIBUTION. Europe (Alps, Carpathians, and SW. Bulgaria); Asia (Kashmir–Himalayan region, SW., NW., and NE. China, U.S.S.R. (Caucasus, C. Asia, W. and E. Siberia, Far East), Mongolia, Korea, Japan); N. America (western part of Canada and the United States).

Eighteen species.

V. Sect. **Gentiana.** Type species: *G. lutea* L.

Sect. *Coelanthae* Froelich, *Gentiana*: 15 (1796). Type species: *G. lutea* L.
Sect. *Gentianotypus* Dumort., *Fl. belg.*: 51 (1827). Type species: *G. lutea* L.
Sect. *Asteria* Gaudin, *Fl. helv.* **2**: 269 (1828). Lectotype species: *G. lutea* L.

Perennials; branching sympodial, the plants with a short, stout rhizome, a non-flowering basal rosette, and a flowering stem; corolla lobed to the middle or below, plicae very small, auriculate, attached to the right side of each lobe as seen from within, or absent (*G. lutea*); seeds with thickened reticulate testa, and a discoid wing.

DISTRIBUTION. C. and S. Europe and S. Norway; Turkey.

Five species.

VI. Sect. **Pneumonanthe** (Gled.) Gaudin, *Fl. helv.* **2**: 269 (1828).

Pneumonanthe Gled., *Syst. pl. stamin. situ*: 238 (1764). Type species: *G. pneumonanthe* L.
Gentiana....Pneumonanthe Link, *Enum. hort. berol. alt.* **1**: 258 (1821). Lectotype species: *G. pneumonanthe* L.
Subgen. *Pneumonanthe* Raf., *Med. fl.* **1**: 208 (1828). Lectotype species: *G. pneumonanthe* L.
Sect. *Cyane* Griseb. in Hook., *Fl. bor.-amer.* **2**: 54 (1837). Type species: *G. pneumonanthe* L.

Perennials; branching sympodial, the plants with a rhizome and 1–few flowering stems, but non-flowering basal rosettes usually absent; flowering stems bearing scale-like leaves below; seed with a reticulately thickened testa, usually winged.

DISTRIBUTION. Much of Europe; N. and E. Asia; N. and C. America.

Thirty-eight species.

VII. Sect. **Phyllocalyx** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 14 (1985). Type species: *G. phyllocalyx* C. B. Clarke.

Sect. *Frigida* β. *Phyllocalyx* Kusn. in *Trudy imp. S.-Peterb. bot. Sada* **15**: 287 (1898).

Perennials; branching sympodial, the plants with short stolons; calyx very small, completely enveloped by the uppermost pair of leaves; stigma-lobes expanded, contiguous into a small disc or infundibuliform structure, but free after anthesis; seeds with honeycomb-like, hexagonal, simple, shallow pits, with a discoid wing.

DISTRIBUTION. C. and E. Himalayan region, mountains of SW. China.

A monotypic section.

VIII. Sect. **Calathianae** Froelich, *Gentiana*: 57 (1796). Lectotype species: *G. nivalis* L.

Hippion F. W. Schmidt, *Fl. boëm.* **2**: 18 (1793). Type species: *H. aestivum* F. W. Schmidt.
Sect. *Ericoila* Dumort., *Fl. belg.*: 51 (1827). Type species: *G. nivalis* L.
Sect. *Gentianella* Gaudin, *Fl. helv.* **2**: 270 (1828), non Dumort. (1827). Lectotype species: *G. nivalis* L.
Sect. *Hippion* (F. W. Schmidt) Gaudin, *Fl. helv.* **2**: 270 (1828).
Sect. *Cyclostigma* Griseb., *Gen. sp. Gent.*: 259 (1838). Lectotype species: *G. nivalis* L.

Perennials, less often annuals; branching sympodial, the plants with stolons and runners; calyx-tube prominently angled or winged; corolla hypocrateriform; stigma-lobes expanded, almost smooth on the surface, contiguous into a disc or infundibuliform structure, but not free after anthesis; seeds usually minutely reticulate, unwinged, rarely reticulately thickened and with a wing at one end.

DISTRIBUTION. W., C., and S. Europe, U.S.S.R. (Arctic European part); W. Asia (Turkey, Iran, Iraq), N. Asia (U.S.S.R. (Caucasus, Altai), Mongolia); N. America (Labrador, Greenland); Africa (Morocco).

Eight species.

IX. Sect. **Ciminalis** (Adans.) Dumort., *Fl. belg.*: 51 (1827).

Ciminalis Adans., *Fam. pl.* **2**: 504 (1763). Lectotype species: *G. acaulis* L.
Sect. *Megalanthe* Gaudin, *Fl. helv.* **2**: 270 (1828). Lectotype species: *G. acaulis* L.
Sect. *Thylacites* Griseb. in DC., *Prodr.* **9**: 115 (1845). Lectotype species: *G. acaulis* L.

Perennials; branching sympodial, the plants with stolons and runners; corolla obconical; stigma-lobes expanded, fimbriate on the surface, contiguous into a small disc or infundibuliform structure, free after anthesis; seeds rugose, with a minutely reticulate testa.

DISTRIBUTION. C. and S. Europe.

Five species.

X. Sect. **Isomeria** Kusn. in *Trudy imp. S.-Peterb. Obshch. Estest.* **24**(2): 196 (1894). Lectotype species: *G. depressa* D. Don.

Perennials; branching sympodial, the plants with stolons and runners; stigma-lobes free, recurved, linear or oblong; seeds with honeycomb-like, hexagonal, simple, shallow pits, rarely with spongy, hexagonal, complex pits.

DISTRIBUTION. Asia (Kashmir–Himalayan region, NE. Burma,

SW., NW., and C. China, U.S.S.R. (E. Siberia, Far East), Japan); N. America (western part of Canada and the United States).

Four series, 18 species.

1. Ser. **Sikkimenses** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 13 (1985).

Sect. *Frigida* ser. *Sikkimenses* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 162 (1937). Type species: *G. sikkimensis* C. B. Clarke.

Leaves obovate, spathulate or oblong, rounded or obtuse at the apex, petioles of cauline leaves gradually broadened towards the top of the stem; flowers in fascicles of 3–8 in a capitate infloresence.

DISTRIBUTION. As for the section, except NW. China.

Six species.

2. Ser. **Depressae** (H. Smith) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 13 (1985).

Sect. *Frigida* ser. *Confertifoliae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 161 (1937). Type species: *G. confertifolia* Marquand.
Sect. *Frigida* subsect. *Sympodiae* ser. *Depressae* H. Smith in *Kew Bull.* **15**(1): 55 (1961). Type species: *G. depressa* D. Don.

Leaves and calyx-lobes with conspicuous cartilaginous margins; flowers usually solitary, terminal.

DISTRIBUTION. C. and E. Himalayan region, SW. and NW. China.

Six species.

3. Ser. **Stragulatae** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 13 (1985). Type species: *G. stragulata* Balf. f. & Forrest ex Marquand.

Calyx-lobes orbicular, spathulate, abruptly contracted at the base into a tongue.

DISTRIBUTION. E. Himalayan region, SW. China.

Two species.

4. Ser. **Uniflorae** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 14 (1985).

Sect. *Frigida* ser. *Uniflorae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 161 (1937). Type species: *G. filistyla* Balf. f. & Forrest ex Marquand.

Flowers solitary, terminal; calyx-lobes narrowly elliptical or triangular.

DISTRIBUTION. Himalayan region, SW. China.

Four species.

XI. Sect. **Microsperma** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 14 (1985). Type species: *G. delavayi* Franchet.

Annuals; capsule oblong; seed with honeycomb-like, hexagonal, simple, shallow pits.

DISTRIBUTION. Nepal, Bhutan, SW. China.

Three series, 10 species.

1. Ser. **Suborbisepalae** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 15 (1985).

Sect. *Frigida* ser. *Suborbisepalae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 160 (1937). Type species: *G. suborbisepala* Marquand.

Leaves and calyx-lobes spathulate; flowers small; gynoecium and stamens usually exserted from the corolla.

DISTRIBUTION. Nepal, Bhutan, SW. China.

Six species.

2. Ser. **Tetramerae** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 15 (1985).

Sect. *Frigida* ser. *Annuae* subser. *Tetramerae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 165 (1937). Type species: *G. lineolata* Franchet.

Flowers 4-merous, medium-sized; calyx-lobes with strongly keeled midribs which are decurrent below into strong wings.

DISTRIBUTION. China (Yunnan, Sichuan).

Two species.

3. Ser. **Annuae** (Marquand) T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 15 (1985).

Sect. *Frigida* ser. *Annuae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 165 (1937). Type species: *G. picta* Franchet ex F. B. Forbes & Hemsley.

Flowers 5-merous, small; calyx-lobes linear or oblanceolate.

DISTRIBUTION. China (Yunnan, Sichuan).

Two species.

XII. Sect. **Stenogyne** Franchet in *Bull. Soc. bot. Fr.* **31**: 375 (1884). Type species: *G. primulaefolia* Franchet.

Annuals, rarely perennials; flowers large or medium-sized; calyx keeled or winged; plicae asymmetrical, extremely oblique; style filiform, longer or slightly shorter than the ovary; seeds usually with a minutely reticulate testa, triquetrous with three winged edges, rarely unwinged or areolate.

DISTRIBUTION. E. Burma, SW., NW., N., C., and S. China, Thailand.

Fourteen species.

XIII. Sect. **Dolichocarpa** T.N. Ho in *Bull. bot. Res. Harbin* **5** (4): 16 (1985). Type species: *G. prostrata* Haenke.

Varasia Philippi, *Fl. atacam.*: 35 (1860). Type species: *V. podocarpa* Philippi.

Annuals; flowers small; plicae symmetrical, large; capsule oblong, unwinged; seeds minutely reticulate, unwinged at maturity, rarely winged when young.

DISTRIBUTION. Europe (E. Alps); Asia (W. Asia (Iran, Afghanistan), Pamir–Himalayan region, SW. and NW. China, U.S.S.R. (Caucasus, Arctic region, C. Asia, W. and E. Siberia, Far East)); N., C., and S. America.

Twelve species.

XIV. Sect. **Chondrophyllae** Bunge in *Nouv. Mém. Soc. imp. Nat. Mosc.* **1**(7): 207, 231 (1829) (Changed to *Chondrophylla* by most later authors). Lectotype species: *G. aquatica* L.

Chondrophylla (Bunge) Nelson in *Bull. Torrey bot. Club* **31**: 245 (1904).
Holubia A. & D. Löve in *An. Inst. bot. A. J. Cavanilles* **32**: 226 (1975), nom. illeg. (Art. 64.1), non *Holubia* Oliver (1884). Type species: *H. pyrenaica* (L.) A. & D. Löve.
Holubogentia A. & D. Löve in *Bot. Notiser.* **131**: 385 (1978), based on *Holubia* A. & D. Löve.

Annuals, rarely perennials; flowers small; plicae symmetrical, large; capsule obovoid or ellipsoid-oblong, conspicuously winged, the wing strong and broad at the apex but gradually narrowed towards the base; seeds minutely reticulate.

DISTRIBUTION. Europe, Asia, America, Morocco, Australia.

Eleven series, 158 species.

1. Ser. **Fimbriatae** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 169 (1937). Lectotype species: *G. panthaica* Burk. The type designation of '*G. recurvata* C. B . Clarke' by Ho (1985) is incorrect (Art. 8) because Marquand's original series circumscription (1937) did not include *G. recurvata.*

Leaves and calyx densely and minutely papillose; calyx-lobes filiform-subulate; plicae usually fimbriate, rarely dentate.

DISTRIBUTION. C. and E. Himalayan region, N. Burma, SW., C., and S. China, Indonesia (Sumatra).

Twenty species.

2. Ser. **Rubicundae** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 171 (1937). Type species: *G. rubicunda* Franchet.

Calyx-lobes filiform; plicae entire or denticulate.

DISTRIBUTION. China (except N. and NE.), Philippines.

Ten species.

3. Ser. **Linearifoliae** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 170 (1937). Type species: *G. aristata* Maxim.

Cauline leaves long and very narrow, at least the uppermost linear or subulate.

DISTRIBUTION. Europe (E. Pyrenees, Carpathians, SW. Bulgaria); Asia (W. Asia (Turkey, Iran, Afghanistan), C. and E. Himalayan region, SW., S., and NW. China, U.S.S.R. (Caucasus)).

Fifteen species.

4. Ser. **Orbiculatae** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 170 (1937). Type species: *G. squarrosa* Ledeb.

Calyx-lobes recurved or patent, rarely erect, ovate or orbicular, rarely lanceolate, contracted at the base.

DISTRIBUTION. Kashmir–Himalayan region, China, U.S.S.R. (C. Asia, W. and E. Siberia, Far East), Mongolia, Korea, Japan, Indian Peninsula, Sri Lanka, Indonesia; E. Australia.

Twenty species.

5. Ser. **Humiles** Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 172 (1937). Lectotype species: *G. leucomelaena* Maxim. ex Kusn. The type designation of '*G. aquatica* L.' by Ho (1985) is incorrect (Art. 8) because Marquand's original circumscription (1937) did not include this species.

Ser. *Pubigerae* Marquand in *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 168 (1937).

Stems ascending or decumbent, usually branched from the base, without a conspicuous main stem, or rarely unbranched; calyx-lobes erect, triangular or lanceolate.

DISTRIBUTION. Europe (Spain); Asia (W. Asia, Kashmir–Himalayan region, Burma, China, U.S.S.R. (Caucasus, C. Asia, W. and E. Siberia), N. Mongolia, Korea, Japan); N. America (western part of Canada and the United States).

Thirty-three species.

6. Ser. **Capitatae** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 18 (1985). Type species: *G. capitata* Buch.-Ham. ex D. Don.

Stems simple, densely papillose, winged or angled and leafless in the lower half; in the upper half much branched with abbreviated internodes, numerous leaves and flowering branches, all congested at the apex of the stem into a subcapitate inflorescence.

DISTRIBUTION. Asia (Kashmir–Himalayan region, N. Burma, SW. China, Indo-China); C. America (Mexico and Guatemala); Africa (Morocco).

Sixteen species.

7. Ser. **Fastigiatae** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 18 (1985). Type species: *G. intricata* Marquand.

Stems fastigiately branched from the base or the middle, the main stem very conspicuous, with lax, more or less corymbosely disposed branches.

DISTRIBUTION. Asia (W. Asia, Pamir–Himalayan region, China, U.S.S.R. (C. Asia, W. and E. Siberia, Far East), Mongolia, Korea, Japan, Indonesia (Sumatra)); western part of N. America.

Twenty-four species.

8. Ser. **Napuliferae** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 18 (1985). Type species: *G. napulifera* Franchet.

Perennials, with slightly fleshy, fusiform roots; leaves herbaceous.

DISTRIBUTION. Bhutan, E. India (Assam), SW., C., and S. China, Thailand, Vietnam.

Three species.

9. Ser. **Coriaceae** T.N. Ho, **ser. nov.** Type species: *G. cruttwellii* H. Smith.

Herba perennis, radicibus fibrosis; folia coriacea.

DISTRIBUTION. S. China (Taiwan), Philippines, Sabah, New Guinea.

Thirteen species.

10. Ser. **Piasezkianae** T.N. Ho in *Bull. bot. Res. Harbin* **5**(4): 18 (1985). Type species: *G. piasezkii* Maxim.

Calyx-lobes with keeled midribs which are decurrent below into conspicuous wings; corolla hypocrateriform; capsule narrowly elliptical, attenuate or obtuse at the apex.

DISTRIBUTION. China (N. Sichuan, Gansu, Shaanxi).

Three species.

11. Ser. **Grandiflorae** Grossh. ex T.N. Ho, **ser. nov.** Type species: *G. grandiflora* Laxm.

Ser. *Grandiflorae* Grossh. in V. Komarov, *Fl. URSS* **18**: 572 (1952), nom. inval. (Art. 36.1).

Herba perennis; flores grandi, 40–55 mm longi; capsula anguste elliptica, apice attenuata vel obtusa.

DISTRIBUTION. U.S.S.R. (W. and E. Siberia, C. Asia), Mongolia.

One species.

XV. Sect. **Fimbricorona** T.N. Ho, **nom. nov.**

Sect. *Eurythalia* (Borkh.) Griseb. in *Götting. gel. Anz.* for 1840 (2): 815 (1840), nom. illeg. (Art. 64.1), non Bunge (1829). Lectotype species: *G. coronata* Royle.

Annuals; corolla bearing a corona of multicellular hairs in the throat; plicae well-developed; capsule obovate, rounded at the apex, winged, the wing strong and broad at the apex but gradually narrowed towards the base of the capsule; seeds minutely reticulate.

DISTRIBUTION. Kashmir–Himalayan region, mountains of SW. China.

Four species.

GEOGRAPHICAL DISTRIBUTION

Gentiana is a subcosmopolitan genus. It is distributed widely in Europe and the temperate zone of Asia and N. America, but a few species extend northwards to the Arctic region (arctic Siberia, Iceland and to 73° N in Greenland), southwards to C. and S. America (the southernmost to Santa Cruz (*c.* 49° 58′S, 69°W), Argentina), through S. Asia to the South Tableland (*c.* 35° 58′S, 149° 25′E) of Australia, and from SW. Europe to Djebel Toubkal in C. Morocco.

There are 14 sections in Asia, eight in Europe, and six in America, comprising 93.3%, 53.3%, and 40% respectively of the world total, while there are 312 species in Asia, 27 in Europe, and 35 in America, comprising 86.4%, 7.5%, and 9.7% respectively of the world total,

In Asia (Table 1) sect. *Ciminalis* is entirely absent; sect. *Gentiana* and sect. *Calathianae* contain only one or two species in this area and are restricted to W. Asia, with a few subspecies scattered as far as Lake Baikal; sect. *Pneumonanthe* also has few (only 12) here. Conversely, the other 11 sections contain their highest numbers of species in Asia, i.e. *Otophora* 12 species in Asia/ 12 species in the world, *Cruciata* 21/21, *Monopodiae* 37/37, *Frigida* 16/18, *Phyllocalyx* 1/1, *Isomeria* 18/18, *Microsperma* 10/10, *Stenogyne* 14/14, *Dolichocarpa* 10/12, *Chondrophyllae* 154/158, and *Fimbricorona* 4/4. Moreover, of these 11 sections, six (*Otophora, Monopodiae, Phyllocalyx, Microsperma, Stenogyne,* and *Fimbricorona*) are endemic to Asia. In respect of species, of the 312 species 299 are endemic to Asia, 95.8% of the total for Asia, and only 13 are common to Asia and Europe or America. It is clear that Asia is the major centre for *Gentiana* with the greatest number of species as well as endemics. The highest concentration of these occurs in the mountains of SW. China (NW. Yunnan, W. Sichuan, and SE. Tibet) and in the NE. Burma area, the square between 25°–34° N and 91°–105° E. In this area there are 11 sections and 190 species, of which 98 are endemic to the mountains of SW. China and the NE. Burma area; thus three quarters of all the sections and half the species of the world occur in this small area, indicating that it is a major centre of diversity and endemism of *Gentiana*. In addition, 10 sections and 61 species (13 of which are local

Table 1 The numbers of species of *Gentiana* in different regions.

	Regions \ Sections	Otophora	Cruciata	Monopodiae	Frigida	Gentiana	Pneumonanthe	Phyllocalyx	Calathianae	Ciminalis	Isomeria	Microsperma	Stenogyne	Dolichocarpa	Chondrophyllae	Fimbricorona	Total
	The world	12	21	37	18	5	38	1	8	5	18	10	14	12	158	4	361
	Total	12	21	37	16	1	12	1	2	–	18	10	14	10	154	4	312
Asia	Mts of SW. China	10	10	25	15	–	–	1	–	–	15	9	9	6	88	2	190
Asia	C. & E. Himalaya	5	3	8	3	–	–	1	–	–	9	2	–	5	23	2	61
	Total	–	2	–	2	5	2	–	8	5	–	–	–	1	2	–	27
Europe	Pyrenees–Alps	–	1	–	2	5	2	–	8	5	–	–	–	1	2	–	26
Europe	Carpathians	–	1	–	1	2	2	–	4	2	–	–	–	–	1	–	13
	Total	–	–	–	1	–	26	–	1	–	1	–	–	3	3	–	35
America	N. America	–	–	–	1	–	20	–	1	–	1	–	–	1	2	–	26
America	C. America	–	–	–	–	–	6	–	–	–	–	–	–	2	1	–	9
America	S. America	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	3
	Africa (Morocco)	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	2
	Australia	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1

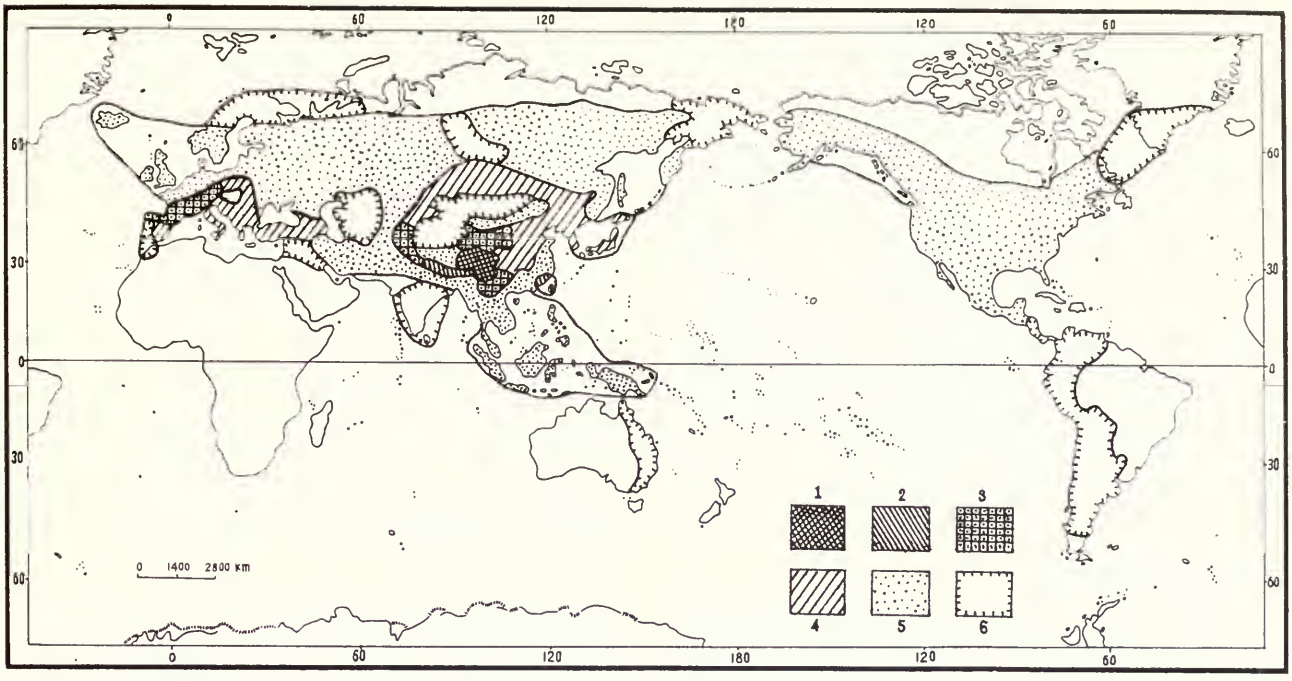

Fig. 5 Isoflor map of species of *Gentiana*. 1. 88–100 species; 2. 60–64 species; 3. 27–42 species; 4. 11–18 species; 5. 4–10 species; 6. 1–3 species.

endemics) are found in the Himalayan region (Bhutan, Sikkim, Nepal, and S. Tibet), which forms a second centre of diversity and endemism. However, the scores drop more sharply in moving from the main centre to the adjacent regions. The isoflor map (Fig. 5) shows the maximum concentration of species and this trend in distribution.

Of the eight sections in Europe, sect. *Cruciata* occurs also in Asia, while three others (*Pneumonanthe, Frigida,* and *Dolichocarpa*) also occur in both Asia and America, and sect. *Chondrophyllae* also occurs in Asia, America, Australia, and Morocco (these sections, however, contain only one or two species each). Sect. *Ciminalis* is a strictly European endemic and sect. *Gentiana* is almost endemic. There are 27 species in Europe, of which 17 are endemic and 10 more widespread. Of the 10 widespread species, all also occur in Asia, but only two reach America and one NW. Africa (Morocco). The maximum concentration of sections and species in Europe is in the Alps and Pyrenees, with 26 species belonging to eight sections; the second concentration is in the Carpathians, with 13 species belonging to seven sections. It is suggested that the floristics of European *Gentiana* is closely related to, and derived from, that of Asia, and has reached its highest development in the most favourable environment of the Alps and Pyrenees.

In America, in contrast to Asia and Europe, there are no endemic sections, all six being widespread; one also occurs in Asia, and the others in Asia and Europe. Five of the six sections (*Frigida, Calathianae, Isomeria, Dolichocarpa,* and *Chondrophyllae*) contain only 1–3 species each. Sect. *Pneumonanthe* contains 26 species in America, more than elsewhere, and all are endemic. There are 35 species in all in America, of which 30 are endemic and five widespread. All five widespread species also occur in Asia, while two occur in Europe as well. The floristics of American *Gentiana* can thus be said to be dominated by sect. *Pneumonanthe* and to be derived from Asia, although there is a lesser development than in Asia, or even than in Europe, without any endemic sections but with more endemic species. Most species occur in N. Ameria (26 species), but some in C. America (9 species) and S. America (3 species). However, there is no obvious centre of diversity, although there are relatively many species (10) in Pennsylvania, Virginia, N. and S. Carolina, Georgia, and Florida.

According to the literature, there is no *Gentiana* in Australia, but we have seen one in SE. Australia, *G. quadrifaria* Blume, a rather common species of Indo-China, Malaya, and Indonesia. The Australian occurrence is clearly an extension from S. Asia. We have also seen specimens of two species from Morocco: *G. brachyphylla* Vill. and *G. atlantica* Litard. & Maire. The former presumably spread from Europe, while the latter is endemic to Morocco.

The geographical patterns within *Gentiana* can be further indicated by the floristic analysis of sections and species. The 15 sections and 361 species may be arranged in 14 geographical elements and variant patterns.

No section is tropical but an overwhelming majority, 14 (about 93.3% of the world total), have a temperate distribution pattern. 326 species (about 90.3% of the world total) have a temperate distribution pattern, and only 35 species (about 9.7%) have a tropical distribution pattern. *Gentiana* is thus a predominantly temperate genus.

Of those sections with a temperate distribution, most (6 sections, 40% of the total) belong to the E. Asia element and to its variant, the Sino-Himalaya element, then to the North temperate element (4 sections), then to the European endemic element (2 sections), Old world temperate element (1 section), E. Asia and N. America disjunct element (1 section) and cosmopolitan element (1 section). The distribution pattern of the species is essentially similar to that of the sections. It is dominated by the E. Asia element, containing 259

species, about 71.8% of the world's total, but the percentage of endemic and stenochorous species is very high, whereas that of the widespread species is quite low. It is clear that these widespread distribution patterns (North temperate, Old world temperate, and E. Asia and N. America disjunct) indicate the relationship between the floras of Asia, Europe, and America. The mountains of SW. China and NE. Burma comprise not only a strong modern centre of distribution, but may also be the main area of origin for the genus, as the greatest number of taxa occur there, as well as probably the primitive type of the genus, sect. *Stenogyne*. Through this primitive section, *Gentiana* shows a certain affinity with *Crawfurdia* and *Tripterospermum*. Sect. *Stenogyne, Crawfurdia,* and *Tripterospermum* share asymmetrical plicae between the corolla-lobes, glands at the base of the ovary, and winged seeds. Their geographical distributions all belong to the E. Asia pattern and most species are centred on the mountains of SW. China and NE. Burma.

The geographical distribution of the sections may be summarized as follows:

A. Wide distribution

1. *Cosmopolitan*. There is only one section with this distribution pattern, *Chondrophyllae*. This section contains some 158 species and has the widest distribution of any section of *Gentiana*. It occurs in Europe, Asia, America, NW. Africa, and Australia. The great majority (154) of species are centred in Asia (especially in the mountains of SW. China and NE. Burma, where there are 88 species) and occur all over Asia, with one species (*G. quadrifaria* Blume) extending to SE. Australia, and another (*G. aquatica* L.) to western North America. There are two species in Europe, three in America, and one in Africa (Morocco). One European species, *G. boryi* Boiss., is endemic to Spain, and another, *G. pyrenaica* L., occurs in the E. Pyrenees, the Carpathians and the mountains of SW. Bulgaria, and extends to W. Asia. Of the three American species, *G. douglasiana* Bong. is endemic to western N. America, *G. pumilio* Standley & Steyerm. is endemic to Guatemala and Mexico, and *G. aquatica* L. occurs in the western part of N. America as well as in N. and W. Asia (Fig. 6). The Moroccan species, *G. atlantica* Litard. & Maire, is endemic to the western coast of that country.

B. Tropical distribution

No section can be described as having a tropical distribution, although a few species do.

C. Temperate distribution

The overwhelming majority of sections and species have various types of temperate distribution pattern.

1. *North temperate pattern*. Four sections have this distribution pattern, which covers Europe and the temperate zone of Asia and N. America.

Sect. *Frigida*. Although this section with 18 species occurs in Europe, Asia, and N. America, there is a disjunction across the eastern European plain of the U.S.S.R. The two western species are endemic to the Alps, Carpathians, and SW. Bulgaria, whereas 16 species occur in the East, Asia, and America. The distribution of these species is centred on the mountains of SW. China and NE. Burma, where of 15 species, ten are extremely local, the others extending both east and west, i.e. one species to the Himalayan region, two just to Qinghai, and one to both Qinghai and the Himalayan region. *G. algida* Pallas, which is more widespread, links the continents of Asia and America, extending from the mountains of SW. China westwards to Sikkim, northwards across NW. China to C. Asia, and through W. and E. Siberia,

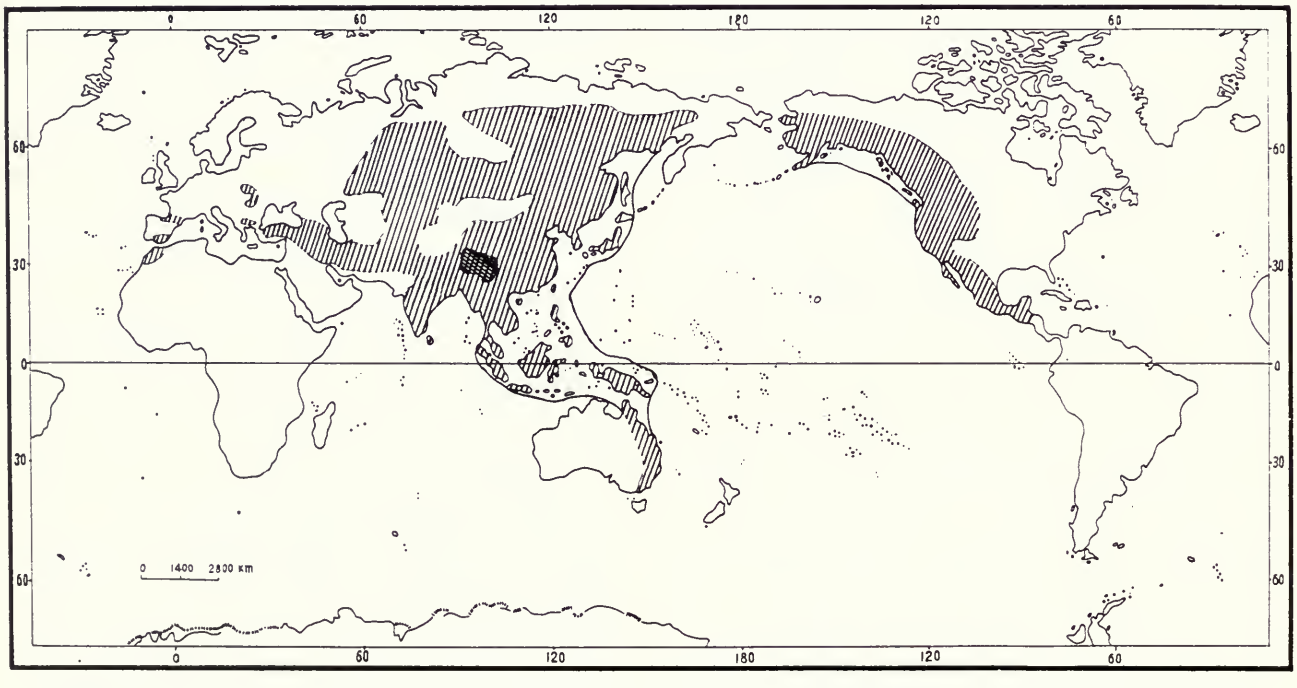

Fig. 6 Distribution area of sect. *Chondrophyllae* Bunge, the cross-hatched area showing the maximum concentration of species.

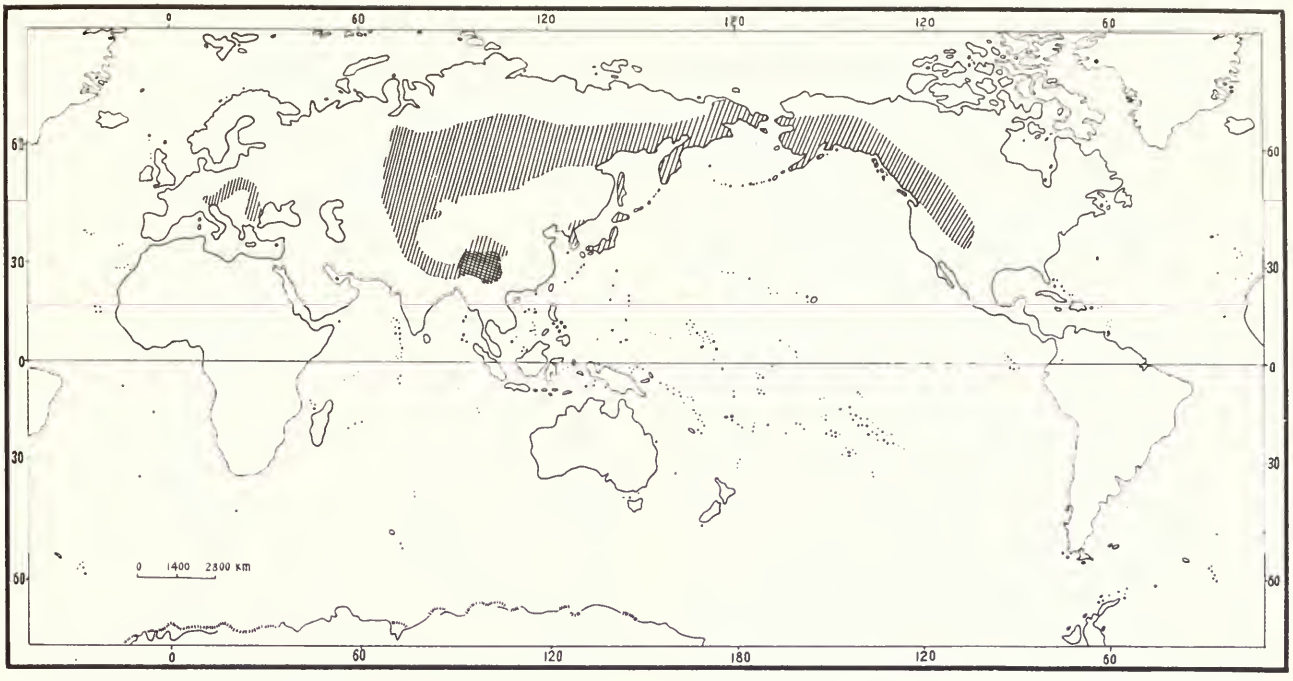

Fig. 7 Distribution area of sect. *Frigida* Kusn., the cross-hatched area showing the maximum concentration of species.

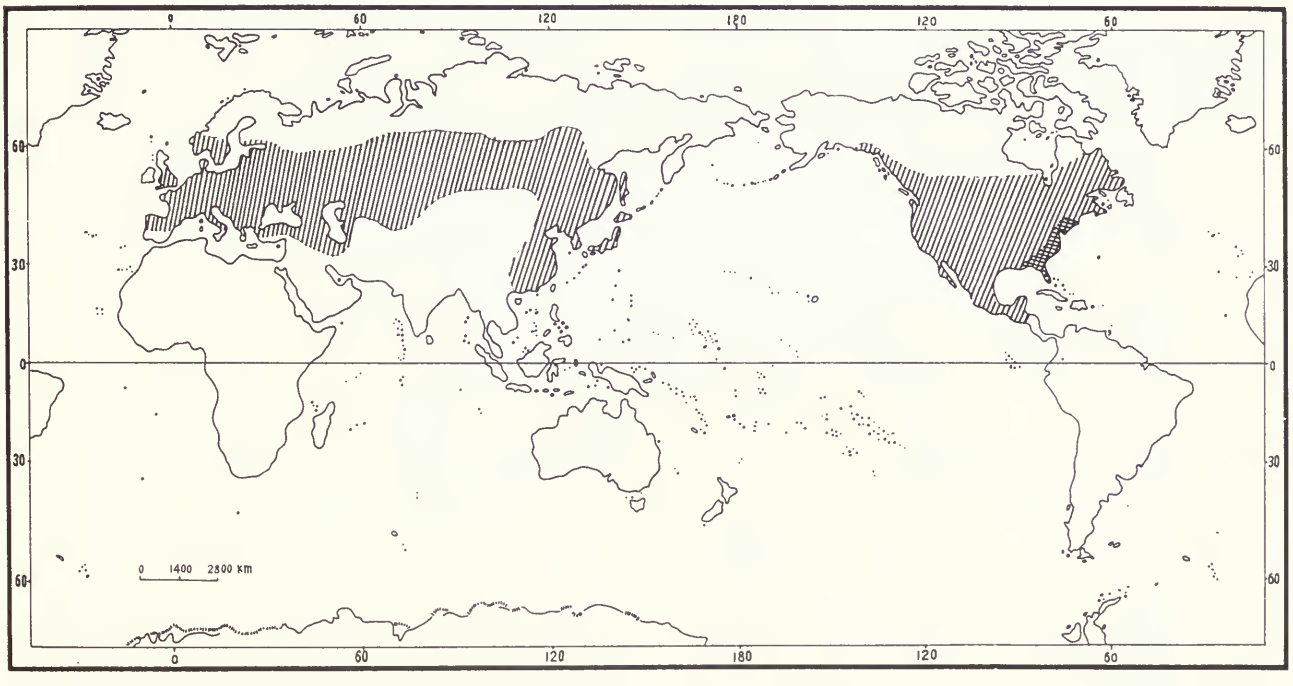

Fig. 8 Distribution area of sect. *Pneumonanthe* (Gled.) Gaudin, the cross-hatched area showing the maximum concentration of species.

Korea, Japan, and the Far East into Alaska, and south along the Rocky Mts to Colorado. *G. apiata* N. E. Br. is restricted to Tai-Pei-Shan of Shaanxi, China (Fig. 7).

Sect. *Pneumonanthe*. This section, consisting of 38 species, is distributed widely through much of Europe, N. and E. Asia, and N. and C. America, and disjunctly in Kamchatka and the Kolyma-Anadyr region of the U.S.S.R. It is centred in America where the majority of species (26) occur, 20 being endemic to N. America and six to C. America. Fewer species (12) occur in Asia and Europe, six being restricted to E. Asia, occurring in NE., N., and E. China, U.S.S.R. (E. Siberia, Far East), Korea, and Japan, four occurring in W. and C. Asia, and two being common to both Asia and Europe,

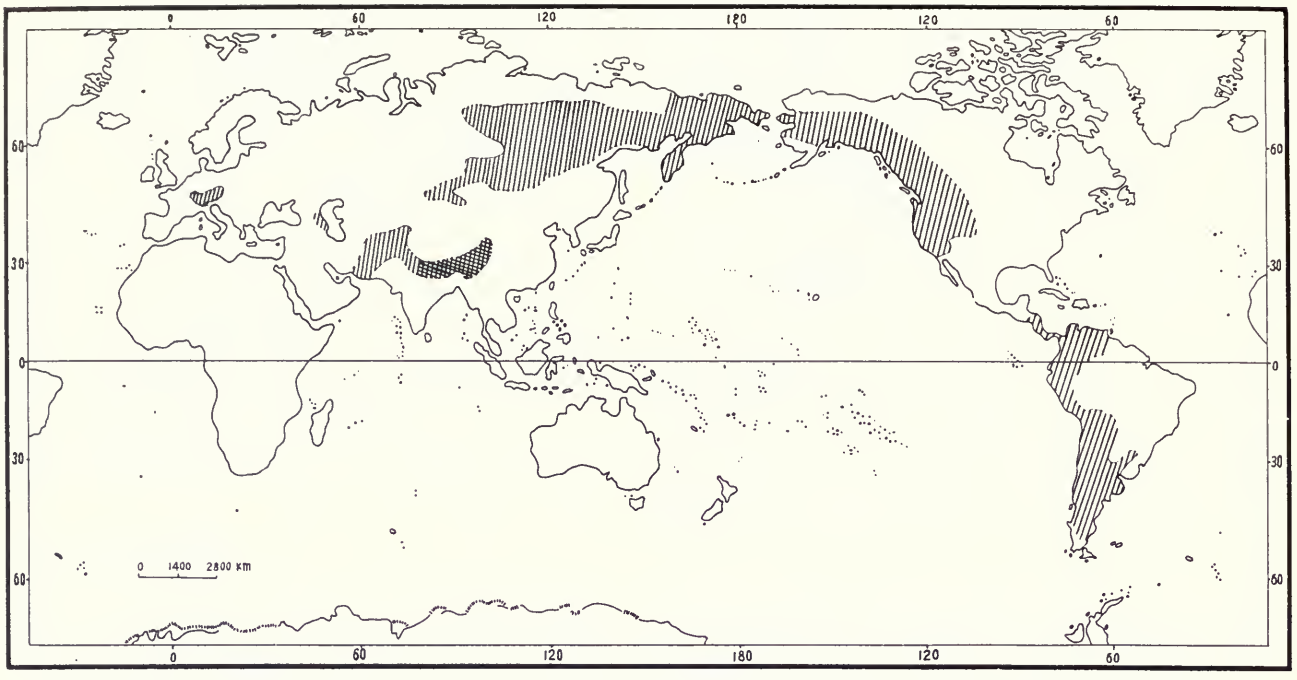

Fig. 9 Distribution area of sect. *Dolichocarpa* T.N. Ho, the cross-hatched area showing the maximum concentration of species.

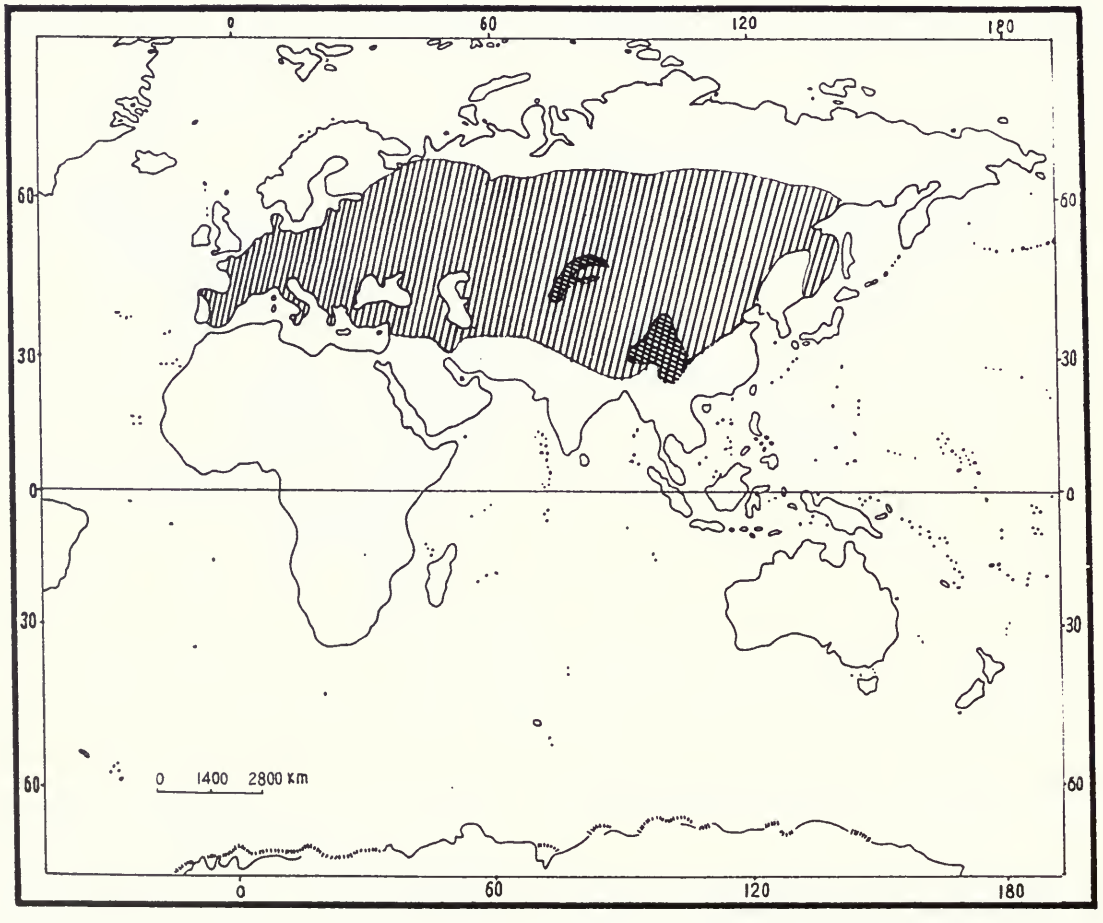

Fig. 10 Distribution area of sect. *Cruciata* Gaudin, the cross-hatched area showing the two subcentres of distribution of the species.

distributed over much of Europe, W. and C. Asia, and W. and E. Siberia (Fig. 8).

Sect. *Calathianae*. This rather small section, comprising eight species and five subspecies, occurs in C., S., and N. Europe, although *G. brachyphylla* Vill. extends south-east to Turkey, Iraq, and N. Iran, and south-west to Morocco, with two subspecies extending further to C. Asia and the Altai; *G. nivalis* L. also extends south-east to Turkey and the Caucasus, as well as north to Labrador in Canada and Greenland to about 73° N, where it reaches the northernmost distribution limit of the genus (Fig. 12–1).

Sect. *Dolichocarpa*. Although this section, with 12 species, belongs to the North temperate pattern, it extends more into South America than the sections mentioned above. It is centred in NW. and SW. China and the Himalayan region, where nine species occur. The three other species occur exclusively outside this area, *G. podocarpa* (Philippi) Griseb. being endemic to South America, *G. sedifolia* Kunth occurring in S. and C. America, and *G. prostrata* Haenke having a remarkably widespread distribution, being scattered interruptedly in the E. Alps, W. Asia, the Caucasus, C. Asia, W. and E. Siberia, the Far East, the Kolyma-Anadyr region, Alaska, and along the mountains of the western part of N., C., and S. America south to Santa Cruz, at about 49° 58′ S, in Argentina (Fig. 9).

2. *Old world temperate pattern*. Only one section has this distribution pattern, which covers Europe and the temperate and cold-temperate zones of Asia.

Sect. *Cruciata*. This section comprises 21 species and has two sub-centres of distribution: the first is in the Himalayan region and the Qinghai-Tibet plateau (including the mountains of SW. China) with 13 species, of which 11 are restricted to this area and two extend eastwards and link the Himalayan region, the Qinghai-Tibet plateau and the north part of China, C. Asia, and E. Siberia; the second is in C. Asia, where three species are endemic and six more widespread, extending east and west and linking Europe, W. Asia, C. Asia, the northern part of China, Siberia, and the Far East. The most widespread of these, *G. cruciata* L., extends west to E., C., and S. Europe, east to W. Siberia, and south-west to W. Asia and the Caucasus. Apart from these species, one other, *G. tenuicaulis* Ling, occurs away from the two sub-centres, in Hebei, China (Fig. 10).

3. *E. Asia and N. America disjunct pattern*. Only one section has this distribution pattern, which covers the temperate and subtropical zones of E. Asia and North America.

Sect. *Isomeria*. This section consists of 18 species. It is centred in the mountains of SW. China and the Himalayan region, where there are 17 species, three of which extend slightly east and south, i.e. *G. chinensis* Kusn., occurring from Sichuan to W. Hubei in China, *G. urnula* H. Smith from E. Tibet to SW. Qinghai, and *G. depressa* D. Don from the Himalayan region, with a disjunct southern area in the Indian Peninsula. The remaining species, *G. glauca* Pallas, is somewhat separated from the main area of distribution and occurs in E. Asia and N. America, extending from Japan, E. Siberia, the Far East, and the Kolyma-Anadyr region into Alaska, the Yukon, and along the Rocky Mts to Montana in the United States (Fig. 11).

4. *E. Asia pattern*. Two sections have this distribution pattern, which covers Kashmir, the Himalaya, China, Korea, Japan, E. Siberia, and the Far East of Russia, extending south to Indonesia.

Sect. *Monopodiae*. This section consists of 37 species and occurs from the Himalayan region and China to Japan, and extends south to Indonesia. The greatest concentration of species occurs in the SW. provinces of China and the Himalayan region (to Kashmir) with 32 species, with two of them

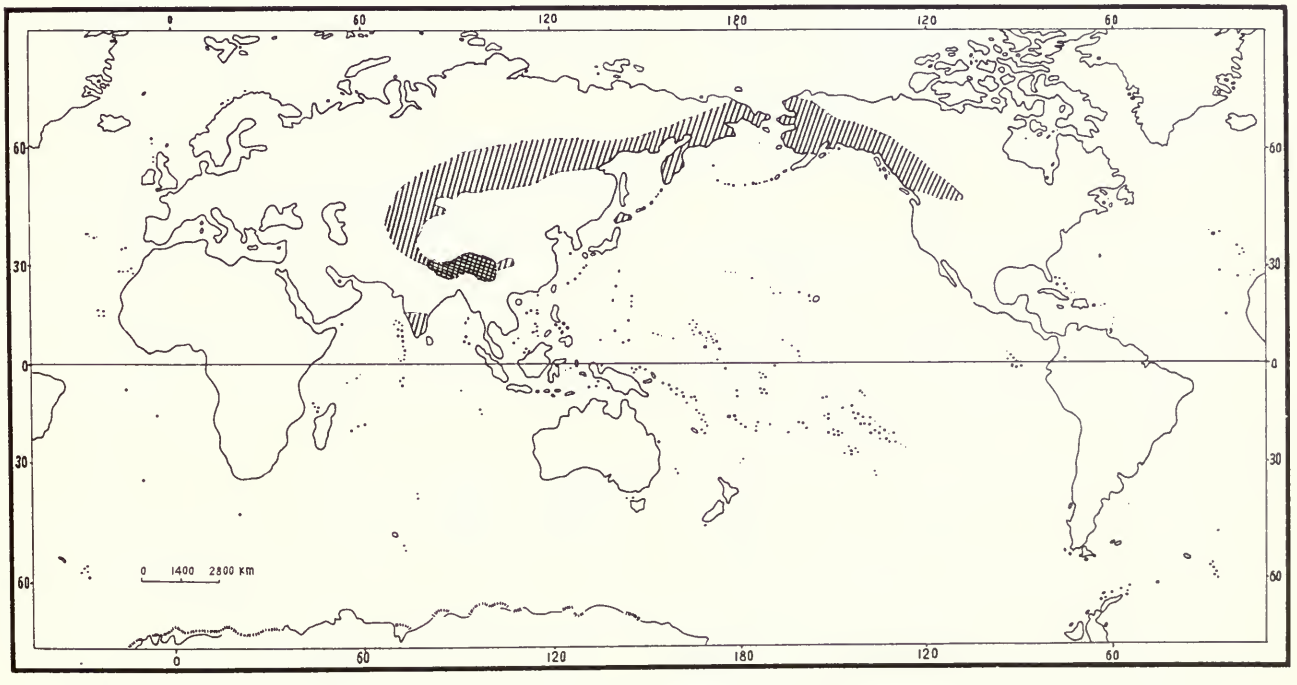

Fig. 11 Distribution area of sect. *Isomeria* Kusn., the cross-hatched area showing the maximum concentration of species.

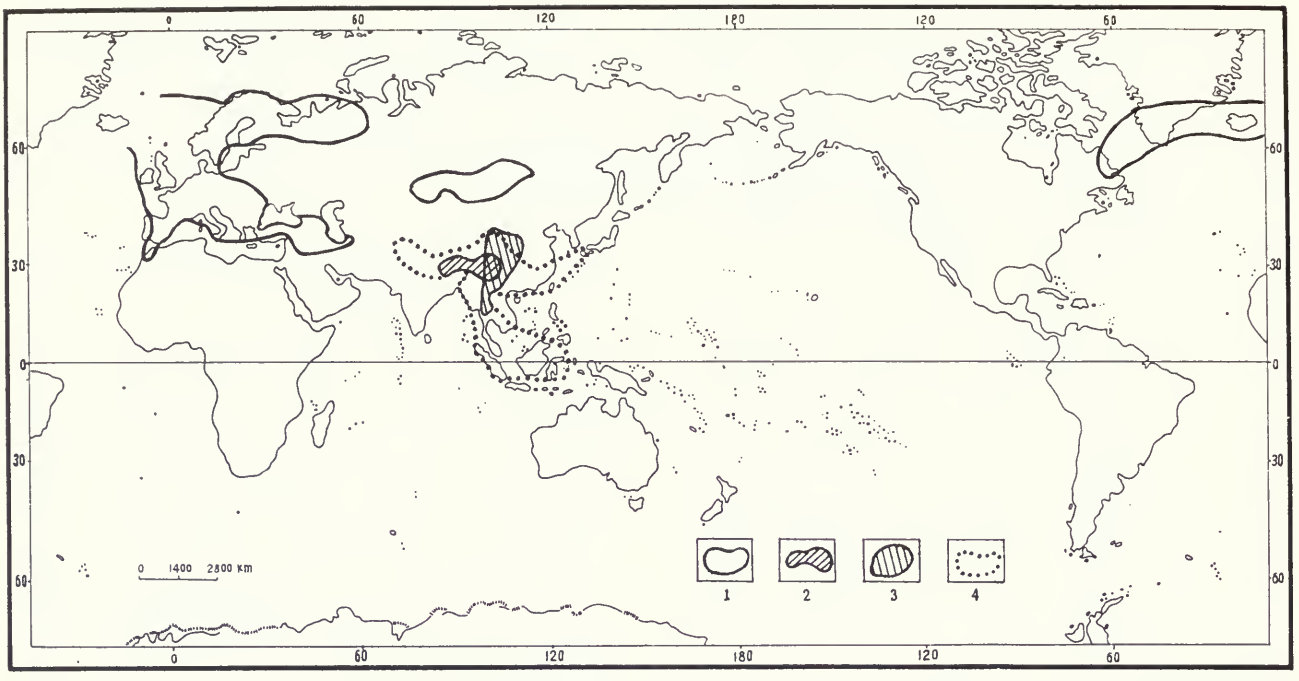

Fig. 12 Distribution areas of sections: 1. *Calathianae* Froelich; 2. *Microsperma* T.N. Ho; 3. *Stenogyne* Franchet; 4. *Monopodiae* (H. Smith) T.N. Ho.

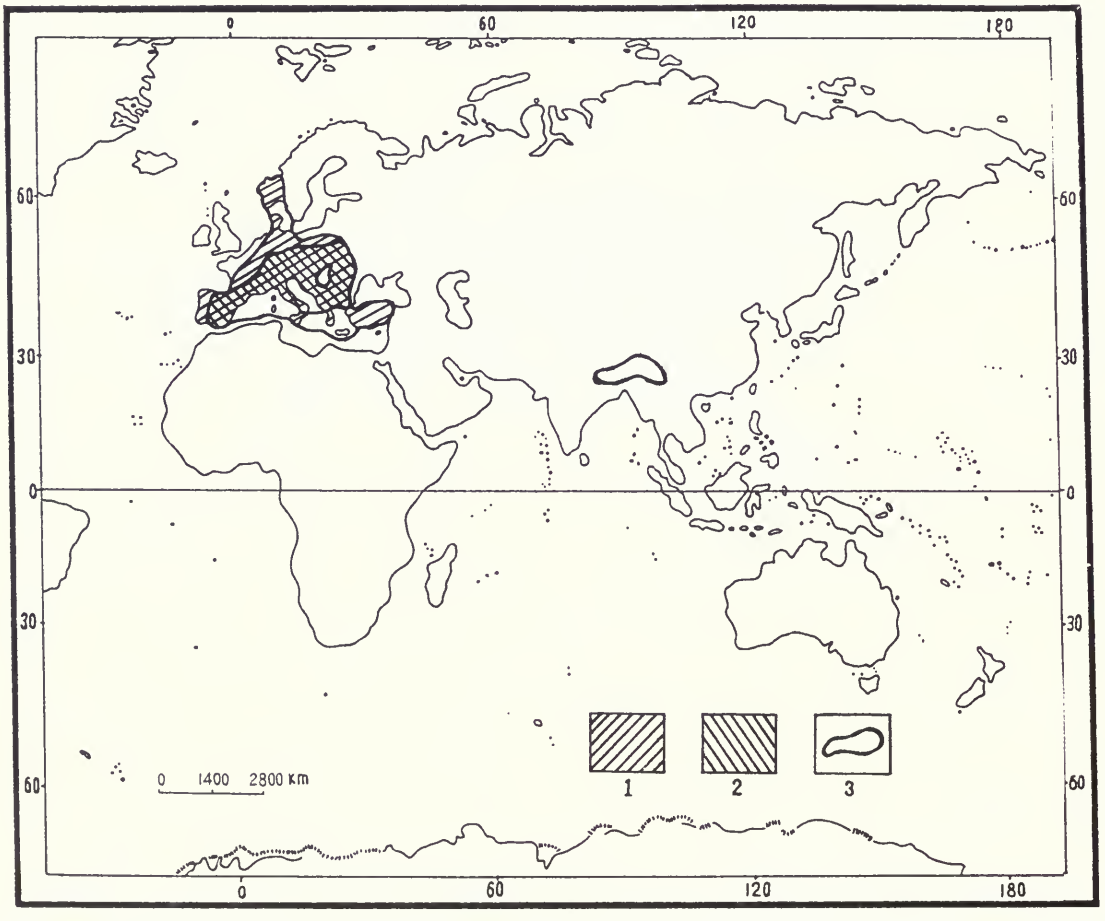

Fig. 13 Distribution areas of sections: 1. *Gentiana*; 2. *Ciminalis* (Adans.) Dumort.; 3. *Phyllocalyx* T.N. Ho and *Otophora* Kusn.

extending from Yunnan in China through Burma to Thailand, and from Guangxi-Zhuang in China to Vietnam. The remaining five species occur exclusively outside the main area and are all endemic, one to Japan and Taiwan, three to Indonesia, and one restricted to S. and E. China, with two varieties in Guizhou, Fujian, and Taiwan (Fig. 12–4).

Sect. *Stenogyne*. This section consists of 14 species, and occurs in SW., NW., N., C., and S. China, E. Burma, and Thailand. It is centred on SW. China where there are 13 species, of which 10 are endemic; three species are more widespread, extending north to SE. Qinghai, S. Gansu, Ningxia-Hui (*G. striata* Maxim.), to S. Shanxi, Henan, Hubei, Guangxi-Zhuang (*G. rhodantha* Franchet ex F. B. Forbes & Hemsley), and south to E. Burma (*G. melvillei* S. Moore). The final species, *G. australis* Craib, is the southernmost of this section, being endemic to Thailand (Fig. 12–3).

Sino-Himalaya variant of the E. Asia distribution pattern. Four sections have this distribution pattern, which covers the area from the mountains of SW. China to the Himalayan region.

Sect. *Otophora*. This section of 12 species has a typical Sino-Himalayan pattern, occurring in the mountains of SW. China and NE. Burma (10 species) and the E. and C. Himalayan region (5 species). It has a marked western distribution (Fig. 13–3).

Sect. *Phyllocalyx*. This monotypic section is restricted to the mountains of SW. China, NE. Burma, and the E. and C. Himalayan region (Fig. 13–3).

Sect. *Microsperma*. This section of 10 species is almost restricted to the SW. provinces of China, being found in Yunnan, Sichuan, SE. Tibet, and Guizhou, but with one species, *G. vernayi* Marquand, extending from SE. Tibet to Nepal (Fig. 12–2), and another, *G. rotundisepala* T.N. Ho, endemic to Nepal and Bhutan.

Sect. *Fimbricorona*. This small section of four species also has a typical Sino-Himalaya pattern. Two species occur from NW. Yunnan and SE. Tibet to Bhutan, and the other two from NW. India (Garhwal, Punjab) to the NW. Himalaya, Kashmir, and Lahul.

5. *Endemic to Europe*. Two sections.

Sect. *Gentiana*. This section with five species is almost endemic to Europe, being centred in the mountains of C. and S. Europe, with *G. purpurea* L. extending to S. Norway, and *G. lutea* to Turkey (Fig. 13–1).

Sect. *Ciminalis*. This section of five species is strictly endemic to Europe, occurring in the mountains of C. and S. Europe, from SW. Germany and the Carpathians to the Alps, Pyrenees, Spain, C. Italy, and SW. Yugoslavia, but is absent from Greece (Fig. 13–2).

STUDY MATERIALS

This study has been based primarily on standard herbarium techniques and on field observations in natural habitats in Yunnan, Sichuan, Tibet, and Qinghai provinces, China.

Nearly 20,000 specimens have been examined from the following herbaria in Europe, China, America, Japan, and Australia, either by visiting these herbaria or by the loan of specimens: A, AU, BM, CANB, CCTC, CIB, COLO, E, FMPI, FUS, FUTU, GMI, HBDB, HGBG, HHBG, HHU, HIB, HMPI, HNDB, HNTC, HNWP, HSNU, IBSC, K, KUN, L, LE, LINN, LZU, MAK, MEL, MO, N, NAS, NK, NY, P, PE, S, SDB, SHM, SMMI, SZ, TI, TIM, UC, UPS, US, W, WH, WU, WUK, YNDB, YUKU, ZHDB, and ZHM.

Acknowledgements. We acknowledge with gratitude the directors of the herbaria listed above for facilities and for the loan of specimens during the preparation of this paper and 'Flora of China, volume 62, Gentianaceae'.

In particular, we are most grateful for the opportunity to make a visit to Great Britain in connection with the *Gentiana* project and extend here our thanks to the Academia Sinica with whose financial support this visit was made by T.N. Ho from March 1986 to May 1987. We sincerely thank the directors and staff of the British Museum (Natural History), the Royal Botanic Gardens, Kew, the Royal Botanic Garden, Edinburgh, and the Linnean Society of London for permission to consult their collections, for facilities provided, and for the loan of specimens. We are much indebted to Mr A. O. Chater and Mr J. F. M. Cannon for many kindnesses, useful discussions, correcting the English manuscript and preparation for publication, and to Mr A. R. Vickery, Dr C. E. Jarvis, Miss C. Whitefoord, Mr F. Nigel Hepper, Miss Sally Bidgood, Dr I. C. Hedge, and Miss Kit Tan for hospitality, much advice and assistance.

We warmly thank the Swedish Institute for enabling T.N. Ho to pursue our research on *Gentiana* in Sweden and we are grateful to Dr R. Moberg and Dr B. Jonsell for arranging this visit.

Many people and organizations, too numerous to name individually here, have helped during the time when we were struggling with the *Gentiana* project. However, special thanks go to the American Rock Garden Society, the Rhododendron Species Foundation of America, the Herbarium of Arnold Arboretum of Harvard University, the United States Herbarium, Department of Botany, Smithsonian Institution, the Herbarium of the Missouri Botanical Garden, and Denver Botanic Gardens for financial assistance or facilities provided, and to Prof. Howard Mason, Mrs Judy Young, Dr Peter S. Ashton, Dr Peter F. Stevens, Dr Peter H. Raven, and Dr Bruce Bartholomew for hospitality and assistance.

Finally, we would like to thank our colleagues Mrs Cui-lan Yan, Mr Jin-jun Liu and Mr Xie-fen Lu for cooperation, illustrations, help with the scanning electron microscopy of seeds, and assistance with field work.

REFERENCES

Czerepanov, S. K. 1973. *Additamenta et corrigenda ad 'Floram URSS' (tomi I-XXX)*. Leningrad. [In Russian; Gentianaceae on pp. 288–292]

Froelich, J. A. 1796. *De Gentiana libellus sistens specierum cognitarum descriptionibus cum observationibus*. Erlangen.

Gilg, E. 1895. Gentianaceae. *In* A. Engler & K. Prantl (Eds), *Die natürlichen Pflanzenfamilien* **4**(2): 50–62. Leipzig.

Gillett, J. M. 1957. A revision of the North American species of *Gentianella* Moench. *Ann. Mo. bot. Gdn* **44**(3): 195–269.

Grisebach, A. H. R. 1838 ['1839']. *Genera et species Gentianearum* ... Stuttgart.

—— 1845. Gentianaceae. *In* A. de Candolle (Ed.), *Prodromus systematis naturalis regni vegetabilis* ... **9**: 38–141. Paris.

Ho, T.-N. 1985. A study on the genus *Gentiana* of China IV. *Bull. bot. Res. Harbin* **5**(4): 1–22.

Ho, T.-N., Liu, S.-W. & Wu, C. J. 1988. Gentianaceae. *Flora reipublicae popularis sinicae* **62**. Beijing.

Holub, J. 1973. New names in Phanerogamae 2. *Folia geobot. phytotax.* **8**: 155–179.

Kusnezow, N. I. 1894. Subgenus *Eugentiana* of genus *Gentiana* Tourn. *Trudy imp. S.-Peterb. Obshch. Estest.* **24**(2): 1–531. [Latin translation in *Trudy imp. S. -Peterb. bot. Sada* **15**: 1–507 (1896–1904)]

—— 1895. *Gentiana* Tourn. *In* A. Engler & K. Prantl (Eds), *Die natürlichen Pflanzenfamilien* **4**(2) : 80–86. Leipzig.

Linnaeus, C. 1737. *Genera plantarum,* ed. 1. Leiden.

—— 1753. *Species plantarum,* ed. 1. Stockholm.

Löve, A. & Löve, D. 1975. The Spanish gentians. *An. Inst. bot. A. J. Cavanilles* **32**(2): 221–232.

Ma, Y. C. 1951. *Gentianopsis*—a new genus of Chinese Gentianaceae. *Acta phytotax.* **1**: 5–19, pls I–V.

Marquand, C. V. B. 1928. New Asiatic gentians. *Bull. misc. Inf. R. bot. Gdns, Kew* for 1928: 49–62.

—— 1931. New Asiatic gentians: II. *Bull. misc. Inf. R. bot. Gdns, Kew* for 1931: 68–88.

—— 1932. The cultivated gentians of China and the Himalaya. *Jl R. hort. Soc.* **57**: 188–211.

—— 1937*a*. The gentians of China. *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 134–180.

—— 1937*b*. Contributions to the gentian flora of southern Tibet, N. E. Burma and Bhutan. *Bull. misc. Inf. R. bot. Gdns, Kew* for 1937: 180–191.

Nilsson, S. 1967. Pollen morphological studies in the Gentianaceae-Gentianinae. *Grana palynol.* **7**: 46–143.

—— 1976. Notes on pollen morphological variation in Gentianaceae-Gentianinae. *Pollen Spores* **9**: 49–58.

Pringle, J. S. 1967. Taxonomy of *Gentiana,* Section *Pneumonanthae,* in eastern North America. *Brittonia* **19**: 1–32.

—— 1977. Taxonomy and distribution of *Gentiana* (Gentianaceae) in Mexico and Central America. I. Sect. *Pneumonanthe*. *Sida Contr. Bot.* **7**(2): 174–217.

—— 1978. Sectional and subgeneric names in *Gentiana* (Gentianaceae). *Sida Contr. Bot.* **7**(3): 232–247.

—— 1979. Taxonomy and distribution of *Gentiana* (Gentianaceae) in Mexico and Central America. II. Sect. *Chondrophyllae*. *Sida Contr. Bot.* **8**(1): 14–33.

Serebryakova, T. I. 1979. Models of shoot formation and some evolutionary trends in the genus *Gentiana* L. *Byull. Mosk. Obshch. Ispyt. Prir., Otdel Biol.* **84**(6): 97–109. [In Russian]

Smith, H. 1936. Gentianaceae. *In* H. Handel-Mazzetti (Ed.), *Symbolae sinicae* **7**: 948–988. Wien.

—— 1961. Problems relating to the *Gentiana cachemirica* of the 'Flora of British India'. *Kew Bull.* **15**(1): 43–55.

—— 1965. Notes on Gentianaceae. *Notes R. bot. Gdn Edinb.* **26**(2): 237–258.

Tournefort, J. P. 1700. *Institutiones rei herbariae. Editio altera,* . . . Paris.

Tutin, T. G. 1972. *Gentiana. In* T. G. Tutin, V. H. Heywood et al. (Eds), *Flora Europaea* **3**: 59–63. Cambridge.

Bull. Br. Mus. nat. Hist. (Bot.) **20**(2): 193–236 Issued 20 December 1990

Revision of *Piper* (Piperaceae) in the New World
2. The taxonomy of *Piper* section *Churumayu*

BRN 864 88

MARGARET CECILIA TEBBS

Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD

CONTENTS

Introduction 194
Distribution and habitat 194
Morphology 194
Habit 194
Leaves 195
Venation 195
Indumentum and pellucid glands 195
Inflorescences 195
Bracts 195
Fruit 195
Section *Churumayu* (Miq.) C. DC. 195
Key to the species in section *Churumayu* 196
Species descriptions 197
21. *Piper guanacostense* C. DC. 197
22. *P. trigonum* C. DC. 197
23. *P. rupununianum* Trel. & Yuncker 199
24. *P. atroglandulosum* Tebbs 200
25. *P. divaricatum* G. Meyer 200
26. *P. dumosum* Rudge 202
27. *P. imberbe* Trel. & Standley 202
28. *P. xylosteoides* (Kunth) Steudel 203
29. *P. urophyllum* C. DC. 204
30. *P. subrepens* Trel. 204
31. *P. mikanianum* (Kunth) Steudel 206
32. *P. carpunya* Ruiz López & Pavón 208
33. *P. grande* M. Vahl 208
34. *P. lepturum* (Kunth) C. DC. 209
35. *P. aequale* M. Vahl 211
36. *P. verruculosum* C. DC. 212
37. *P. corrugatum* Kuntze 213
38. *P. schiedeanum* Steudel 213
39. *P. cadenaensis* Tebbs 218
40. *P. regnellii* (Miq.) C. DC. 219
41. *P. veraguense* C. DC. 221
42. *P. perbrevicaule* Yuncker 223
43. *P. reptabundum* C. DC. 223
44. *P. fortunaensis* Tebbs 223
45. *P. dolichotrichum* Yuncker 225
46. *P. subsessilifolium* C. DC. 225
47. *P. brachypodon* (Benth.) C. DC. 227
48. *P. xanthostachyum* C. DC. 227
49. *P. ottoniifolium* C. DC. 229
50. *P. septuplinervium* (Miq.) C. DC. 231
51. *P. coruscans* Kunth 232
52. *P. scutilimbum* C. DC. 232
53. *P. auritum* Kunth 234
References 236
Index 237

Synopsis. The paper presents a taxonomic treatment of *Piper* section *Churumayu*, and 33 species are recognized, keyed, and described. There are two new species, *P. cadenaensis* Tebbs and *P. fortunaensis* Tebbs, and the new name *P. atroglandulosum* Tebbs is proposed for *P. obovatum* Ruiz López & Pavón.

INTRODUCTION

This second part of a revision of New World species of *Piper* deals with section *Churumayu* (Miq.) C. DC.; see Tebbs (1989*a*) for part 1 which deals with section *Macrostachys*. Section *Churumayu*, as accepted here, is essentially Miquel's (1844) *Artanthe* section *Churumayu* which he describes as 'Petioli nudi. Folia rotundato-vel ovato-oblonga, inf. aequilatera, saepe cordata, sup. basi inaequali rotundata, costis versus basin approximatis, supra glabra, raro puberula'. Although it is regrettable that he defines his section by leaf characters alone, the types of inflorescences, bracts, and fruits in at least half of his species conform with those of the taxa covered in the present treatment. The species accepted in section *Churumayu* have slender, erect, arching or pendulous inflorescences, fleshy orbicular to triangular bracts, and small, trigonous, obovoid fruits, sometimes with a minute style. Prophylls are usually prominent and often several centimetres long. In this treatment, 33 species have been accepted in section *Churumayu*, and 128 names have been reduced to synonymy. The species are differentiated using inflorescence characters supported by vegetative characters, habitat, and general distribution. To this end many specimens, including type material, have been examined, and the full extent of the variation in the section has become apparent. Many of the problems encountered in attempts to define the species limits in *Piper* are due to the wide and frequently continuous range of variation in characters such as leaf size and pubescence density. Narrow taxonomic concepts that give undue weight to these characters, such as those adopted by Trelease (1927, 1929), and to a lesser extent by de Candolle (1869), only serve to create many new and unnecessary taxa, adding to the general confusion within the genus. As in the first part of this treatment of *Piper* (Tebbs, 1989*a*), I have attempted to minimise and clarify this confusion by adopting a broad species concept. This is reflected in the extensive synonymies included under the species accepted here.

I question the taxonomic value of varieties based on vegetative characters in a genus that is phenotypically plastic. Trelease & Yuncker (1950) described many new varieties in their treatment of *Piper*. For example, *P. ottoniifolium* C. DC. was separated by them into var. *frutescens* Trel. & Yuncker, a shrub with leaves 12–15 cm long and 5.5–6 cm wide, and var. *latifolium* Trel. & Yuncker, a scandent shrub with leaves 15–22 cm long and 6–9.5 cm wide. So many intermediate forms can be found in the characters used to distinguish these varieties that it becomes pointless to attempt to separate them. Clearly, the characters popularly employed in the past to segregate varieties, such as slight differences in habit, leaf shape, or the presence or absence of indumentum, overlap too much to be used with any certainty, and no varieties are recognized in this revision.

DISTRIBUTION AND HABITAT

Piper species are usually plants of moist shady ground in disturbed places, and are often rapid colonisers of road- and trail-sides, edges of pasture, and forest clearings. Most species in section *Churumayu* follow this general pattern, and can be found at altitudes ranging from sea-level to more than 2000 m. For example, *Piper guanacostense* C. DC. is confined to the drier Pacific slopes of Costa Rica, growing from 0–1000 m, in fairly close proximity to the coast in shady moist soil at forest edges, while the widespread *P. schiedeanum* Steudel ranges from Mexico to Brazil, growing in a variety of disturbed places from 0–1600 m. *Piper aequale* M. Vahl, *P. dolichotrichum* Yuncker, *P. grande* M. Vahl, *P. ottoniifolium*, *P. subsessilifolium* C. DC., *P. veraguense* C. DC., and *P. xanthostachyum* C. DC. typically occur in moist forest or damp shady places of remnant forest in areas cleared for pasture, from sea-level to over 2000 m. *Piper brachypodon* (Benth.) C. DC. is confined to lowland areas of Nariño Province in Colombia (including Isla Gorgona), where it grows in dense moist forest. *Piper septuplinervium* (Miq.) C. DC. is a plant of brackish places, often growing in mangrove swamps and on riverbanks near the coasts of Colombia and Ecuador, while *P. coruscans* Kunth occurs on high, wet, steep slopes and cliff bases, from Colombia to Brazil. *Piper verruculosum* C. DC. is only found in Costa Rica, growing in the shade of cloud forests between 800–1800 m. *Piper scutilimbum* C. DC. also occurs in cloud forest, but is more widely distributed, from Panama to Ecuador. Two species, *P. mikanianum* (Kunth) Steudel and *P. regnellii* (Miq.) C. DC., have a more southerly distribution than the others in this section and are found at 400–1300 m altitude, from Brazil to Argentina. *Piper mikanianum* grows in gallery forest, while *P. regnellii* can be found on steep wooded slopes, boggy ground, and streamsides. *Piper auritum* Kunth is a successful coloniser of tracksides, clearings, riverbanks, and ground disturbed by landslides, and ranges from Mexico to the West Indies and Colombia, while *P. subrepens* Trel. is a rare species only found on mountain slopes between 700 and 800 m, in Coclé Province, Panama.

MORPHOLOGY

Habit

The majority of species in section *Churumayu* are shrubs or slender trees, with erect to spreading branches. *Piper auritum* forms a thin-trunked tree some 6 m in height, while *P. verruculosum* is a densely branching shrub 1–3 m high. *Piper mikanianum* is a spreading or decumbent shrub with branches

that root at the lower nodes, as do those of *P. urophyllum* C. DC. Five species, *P. dolichotrichum*, *P. ottoniifolium*, *P. reptabundum* C. DC., *P. subsessilifolium* and *P. xanthostachyum*, are true climbers or scramblers, with copious adventitious roots at the nodes that attach the stems to a support (Tebbs, 1989*b*). One species, *P. perbrevicaule* Yuncker, is a terrestrial, sometimes epiphytic, trailing herb often rooting at the nodes.

Leaves

As in the rest of the genus, leaves of the species belonging to section *Churumayu* are very variable in shape and size. *Piper guanacostense* and *P. trigonum* C. DC. have elliptic-oblong to lanceolate leaves, *P. urophyllum* has elliptic leaves that narrow abruptly to a long slender apex, while those of *P. auritum* are asymmetrically oblong-cordate and may reach 55 cm in length. *Piper schiedeanum* is an example of a species in this section displaying a confusing variety of leaf shapes, from ovate-elliptic or lanceolate to deeply cordiform. The leaves often vary on the same plant, and older leaves may be wider and have more prominent basal lobing than juvenile foliage. This variation in leaf shape has resulted in many superfluous taxa being described. Gomez Pompa (1966) has examined the variable shapes of the leaves and the number of secondary veins in *P. schiedeanum*, and on this basis has sunk several taxa into synonymy. Two species, *P. scutilimbum* and *P. veraguense*, have distinctive peltate leaves.

There is a certain amount of variation between species in thickness and texture of the leaves. *Piper auritum* has membranous leaves, while those of *P. carpunya* Ruiz López & Pavón and *P. ottoniifolium* are coriaceous. *Piper corrugatum* Kuntze and *P. perbrevicaule* often have bullate or rugose leaf surfaces.

The petioles range from a few millimetres to 5 cm long, and may be vaginate at the base, e.g. *P. corrugatum*, or partially or wholly sheathing, e.g. *P. auritum*, *P. regnellii*.

Venation

Most species in this section have 1–5 pairs of secondary veins arising from, or near, the leaf base, and 1–3 pairs of veins arising from the middle to upper part of the midrib. The number of basal veins is related to the shape and extent of lobing of the leaf base. Several species, e.g. *P. guanacostense* and *P. trigonum*, have leaves with secondary veins arising along the length of the midrib, indicating a phylogenetic relationship with *P. arboreum* Aublet, of section *Macrostachys*. The venation of *P. ottoniifolium* is distinctly camptodromous, with secondary veins curving strongly from, or near, the base to the apex.

Indumentum and pellucid glands

The hairs found in *Piper* are simple, either unicellular or multicellular. Several species, e.g. *P. dolichotrichum* and *P. perbrevicaule*, have stems and leaves that are densely covered with multicellular hairs 1–3 mm long. *Piper regnellii* and *P. subsessilifolium* are often minutely pubescent on young growth and undersides of leaves. The leaf margins of *P. auritum* are fringed with minute pale hairs, a character that is also found in *P. marginatum* Jacq.

Prominent pellucid glands are quite common in *Piper*, and may be pale yellow, orange, red, brown, or black. The leaves of *P. trigonum* have both hairs and conspicuous pellucid glands. *Piper atroglandulosum* Tebbs has copious black glands on the stems and leaves. *Piper ottoniifolium* has pale glands on the floral bracts and the fruits.

Inflorescences

The inflorescences are mostly erect in section *Churumayu*, e.g. *Piper aequale* and *P. schiedeanum*. *P. auritum* has erect or slightly arching spikes, another character that indicates its relationship with *P. marginatum*. There are several species in which the inflorescences become pendulous with maturity. This is mainly because they are borne on long, thin peduncles, which bend under the weight of the developing fruit (e.g. those of *P. dolichotrichum* and *P. reptabundum*). The floral parts are closely congested in this section, and difficult to segregate. Burger (1972) indicates that the development of slender congested inflorescences can be associated with the activities of small bees, which collect pollen from the surface of the spike.

There is a limited amount of colour variation between species in section *Churumayu*. *P. subsessilifolium* has pink to maroon inflorescences, while those of *P. xanthostachyum* are yellow-white. Generally, however, most of the species treated here have greenish-yellow to dull white spikes.

Bracts

The floral bracts found in this section are triangular to round, often fleshy and glabrous, glandular or pubescent. Several species have bracts that partially cover the fruit, at least in early stages of development, e.g. *P. schiedeanum* and *P. veraguense*. The distinctive bracts of *P. grande* are glabrous, umbonate, and completely cover the developing fruits.

Fruit

The fruits in this section are trigonous and obovoid with angular sides, on average about 1 mm across, with occasionally a domed apex with a minute, scarcely noticeable style. The exception is *P. coruscans* with fruits that become orbicular as they mature. There are 2–4 slender stigmas. Fruits may be glabrous, e.g. *P. aequale*, minutely pubescent, e.g. *P. verruculosum*, or with prominent pellucid glands, e.g. *P. brachypodon*. A few species have a mealy or granular surface, e.g. *P. trigonum*. Species with small trigonous fruits can also be found in section *Radula*, e.g. *P. dilatatum* C. DC. and *P. lanceifolium* Kunth. However, these species also display other characters that are diagnostic of that section, such as dark, often scabrous leaves, dense indumentum, and stipule-like developments on the bases of the petioles, and on that basis are excluded from section *Churumayu*.

Section CHURUMAYU (Miq.) C. DC.

Type: *Piper churumayu* Poeppig

Herbs, shrubs, and trees, scramblers or climbers, rarely epiphytic, glabrous, minutely to densely pubescent or glandular. Leaves ovate, ovate-elliptic to lanceolate, or deeply asymmetrically oblong-cordate to regularly cordiform, occasionally peltate, glabrous, or minutely to densely pubescent or glandular with yellow, orange, brown, or black glands, glossy above, sometimes glaucous or coriaceous. Venation

with 1–8 pairs of secondary veins arising from or near base, and 1–3 pairs from middle to upper part of midrib. Petioles vaginate at the base, or partially to completely sheathing the stem. Prophylls prominent, narrow to wide, acute or blunt-tipped, glabrous, glandular, or pubescent. Inflorescences erect, sometimes arching, or pendulous on long, slender peduncles; flowers densely crowded on rachis. Floral bracts orbicular, crescent-shaped, triangular or T-shaped, sometimes umbonate, fleshy, glabrous, minutely ciliate or with dense margins of hairs, sometimes partially or completely covering developing fruits. Anthers minute, dehiscing laterally or upward. Fruits obovoid, trigonous, rarely suborbicular, glabrous, glandular, granular, or minutely puberulent, occasionally with domed apex and minute style; stigmas 2–4.

Key to the species in section *Churumayu*

1a. Climbers or scramblers:
2a. Inflorescences on long slender peduncles, pendulous in fruit:
3a. Leaves asymmetrically lanceolate to oblong-elliptic, glabrous ..... 43. **P. reptabundum**
3b. Leaves symmetrical, broadly ovate to elliptic, densely long-pubescent ..... 45. **P. dolichotrichum**

2b. Inflorescences not on long slender peduncles, erect:
4a. Leaves coriaceous, with 2–3 pairs of prominent secondary veins arising from base and curving to apex ..... 49. **P. ottoniifolium**
4b. Leaves membranous, with 3–5 pairs of secondary veins arising from near the base to middle part of midrib, ascending rather sharply to apex:
5a. Inflorescences pink or maroon; bracts 0.6–1 mm wide, pink-to purple-ciliate ..... 46. **P. subsessilifolium**
5b. Inflorescences yellow-white; bracts 0.3–0.5 mm wide, yellow-white-ciliate ..... 48. **P. xanthostachyum**

1b. Herbs, shrubs or trees:
6a. Herbs, erect or prostrate:
7a. Stems erect, 1–2 m high, glabrous; leaves peltate; inflorescences 7–16 cm long, on short peduncles ..... 41. **P. veraguense**
7b. Stems prostrate or trailing, 15–50 cm long, pubescent; leaves not peltate; inflorescences 2–4 cm long, on long slender peduncles ..... 42. **P. perbrevicaule**

6b. Shrubs or trees:
8a. Petioles sheathing the stems:
9a. Leaves peltate, base cuneate or caudate ..... 52. **P. scutilimbum**
9b. Leaves not peltate, base shallowly to deeply cordate:
10a. Leaves deeply unevenly cordate with one basal lobe conspicuously lower than other, margins densely ciliate; inflorescences arching ..... 53. **P. auritum**
10b. Leaves widely shallowly cordate, margins glabrous; inflorescences erect ..... 40. **P. regnellii**
8b. Petioles not sheathing the stems:
11a. Floral bracts partially or completely concealing fruits:
12a. Floral bracts umbonate, completely concealing fruits ..... 33. **P. grande**
12b. Floral bracts not umbonate, only partially concealing fruits:
13a. Leaves symmetrically ovate to broadly, evenly cordiform, glabrous; floral bracts 0.4–0.7 mm, orbicular-triangular, fleshy, glabrous or minutely ciliate ..... 38. **P. schiedeanum**
13b. Leaves asymmetrically oblong-cordate to subcordate, glabrous or with long multicellular hairs, sometimes bullate; floral bracts 0.2–0.5 mm, oblong-triangular, upper part slightly protruding, minutely pubescent below ..... 37. **P. corrugatum**

11b. Floral bracts neither completely nor partially concealing fruits:
14a. Fruits shortly pubescent or minutely granular:
15a. Leaves asymmetrically narrowly to broadly elliptic; floral bracts oblong-triangular with gibbous bases ..... 44. **P. fortunaensis**
15b. Leaves symmetrically ovate- or oblong-elliptic; floral bracts triangular, glabrous to densely ciliate:
16a. Stems with tubercles; leaves glabrous on both surfaces, eglandular ..... 32. **P. carpunya**
16b. Stems smooth, without tubercles; leaves puberulent on undersurfaces, with prominent orange or brown glands:
17a. Leaves with 3–4 pairs of secondary veins; peduncles 15–30 mm long ..... 23. **P. rupununianum**
17b. Leaves with 4–7 pairs of secondary veins; peduncles 6–15 mm long ..... 22. **P. trigonum**

14b. Fruits glabrous:
18a. Fruits with pellucid glands visible on upper surface:
19a. Stems and leaves red-streaked, eglandular; veins prominent ..... 47. **P. brachypodon**
19b. Stems and leaves with copious glands; veins faint:
20a. Leaves oblanceolate ... 24. **P. atroglandulosum**
20b. Leaves ovate-lanceolate to oblong-elliptic:
21a. Leaves glabrous:
22a. Leaves membranous, apex long-acuminate ..... 34. **P. lepturum**
22b. Leaves subcoriaceous, apex acute, blunt ..... 25. **P. divaricatum**
21b. Leaves sparsely to moderately pubescent ..... 26. **P. dumosum**

18b. Fruits without pellucid glands visible on upper surface:
23a. Leaves lanceolate to narrowly elliptic:
24a. Fruits glabrous ..... 35. **P. aequale**
24b. Fruits pubescent:
25a. Leaves with orange or brown glands ..... 36. **P. verruculosum**
25b. Leaves eglandular . 39. **P. cadenaensis**

23b. Leaves ovate, sub-orbiculate, ovate-elliptic, base obtuse to cordate or subcordate:
26a. Leaves sub-orbiculate; fruits sub-orbicular ..... 51. **P. coruscans**
26b. Leaves not sub-orbiculate; fruits trigonous:
27a. Subshrubs, spreading or decumbent, 0.5–1 m high:
28a. Leaves peltate ..... 27. **P. imberbe**
28b. Leaves not peltate ..... 31. **P. mikanianum**

27b. Shrubs, erect, at least 1 m high:
29a. Floral bracts T-shaped ... 50. **P. septuplinervium**
29b. Floral bracts not T-shaped:
30a. Leaf bases thickened, forming dark 'lips'; fruits 1–2 mm wide ..... 29. **P. urophyllum**

30b. Leaf bases not thickened; fruits 0.5–1 mm wide:
31a. Leaves with scattered glands; floral bracts glabrous .... 28. **P. xylosteoides**
31b. Leaves eglandular; floral bracts minutely ciliate:
32a. Inflorescences 2–3 cm long .... 30. **P. subrepens**
32b. Inflorescences 3–9 cm long ..... 21. **P. guanacostense**

SPECIES DESCRIPTIONS

21. **Piper guanacostense** C. DC. in *Linnaea* **37**: 356 (1872). Type: Costa Rica, *Oersted* 862 (C!-holotype).
Fig. 2A, a, b.

Shrubs or slender trees, 1–3 m high, glabrous or minutely puberulent. Leaves 10–14 (–18) cm long, 3–5 cm wide, lanceolate, glossy, apex acuminate, base acute to obtuse, glabrous. Venation with 6–12 pairs of secondary veins arising along the length of the midrib, loop-connecting to the apex. Petioles 3–10 mm long. Prophylls 4–12 mm long, glabrous. Inflorescences 3–9 cm long; peduncles 6–12 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.7 mm wide, triangular, ciliate. Fruits obovoid, 1 mm wide, trigonous to orbicular, glabrous; stigmas sessile.

Growing in shade in moist places or along streams; 0–1000 m.

DISTRIBUTION. Costa Rica. Fig. 1.

Costa Rica, Guanacaste: *Liesner* 5013 (MO); Puntarenas: *Burger & Ramirez* 4044 (F, BM).

Piper guanacostense is restricted to the Pacific side of Costa Rica and grows in the shade of moist forest on hills fairly close to the coast. It has similar leaf shape and venation to that of *Piper arboreum* Aublet, but does not have that species' sheathing petioles, and the inflorescence is erect rather than pendulous. Unlike *P. arboreum* it has a well-developed prophyll.

Piper guanacostense, along with *P. atroglandulosum* and *P. trigonum*, can be distinguished from other species in this section by its distinctly pinnate venation loop-connecting to the apex, lacking the prominent pairs of veins arising from the base of the leaf. The glabrous fruits distinguish it from *P. trigonum*, which has glandular, pubescent, or granular fruits.

Fig. 1 Distribution of *P. guanacostense*.

22. **Piper trigonum** C. DC. in *J. Bot., Lond.* **4**: 212 (1866). Type: Colombia, Prov. Barbacoas, *Triana* 44 (G-holotype; BM!-isotype).
Fig. 2B, c, d.

P. schlimii C. DC., in DC., *Prodr.* **16**(1): 274 (1869). Type: Venezuela, *Funcke & Schlim* 591 (G-holotype; BM!-isotype).
P. arieianum C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 166 (1897). Type: Costa Rica, Bords de l'Ariei, Talamanca, *Pittier* 9387 (G-holotype; MO!-photograph).
P. saltuum C. DC. in Urban *Symb. antill.* **7**: 185 (1912). Type: Trinidad, Cuparo, *Broadway* 3207 (G-holotype).
P. acutissimum Trel. in *Contr. U.S. natn. Herb.* **26**: 25 (1927). Type: Panama, Chagres, prov. Colon, *Fendler* 266 (US-holotype; K!, MO!-isotypes).
P. trichopus Trel. in *Contr. U.S. natn. Herb.* **26**: 25 (1927). Type: Panama, *Sutton Hayes* 797 (NY!-holotype).
P. altevaginans Trel. in *Contr. U.S. natn. Herb.* **26**: 140 (1929). Type: Costa Rica, Guapiles, Limón, *Standley* 37316 (US-holotype).
P. generalense Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 344 (1937). Type: Costa Rica, vicinity of El General, prov. San José, *Skutch* 2846 (US-holotype; NY!-isotype).
P. marginatibaccum Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 349 (1937). Type: Costa Rica, vic. of El General, San José, *Skutch* 2183 (US-holotype; MO!, NY!-isotypes).
P. seducentifolium Trel. in *Ann. Mo. bot. Gdn* **27**: 297 (1940). Type: Panama, *Woodson* et al. 781 (MO!-holotype).
P. acutissimum var. *trichopus* (Trel.) Yuncker in *Ann. Mo. bot. Gdn* **37**: 66 (1950). Type as for *P. trichopus*.
P. gorgonae-insulae Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 331 (1950). Type: Colombia, south end of Gorgona Island, Nariña, *Killip & Garcia* 33095 (US-holotype; BM!-isotype).
P. portachueloense Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 327 (1950). Type: Venezuela, El Portachuelo, Aragua, *Pittier* 11815 (US- holotype; NY!-isotype).
P. riitosense Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 396 (1950). Type: Venezuela, Aragua, *Killip & Lasser* 37755 (US-holotype, photograph!).

Shrub 0.5–1 (–2) m high, stems minutely pubescent, especially on younger growth. Leaves 10–20 cm long, 3–6.5 cm wide, elliptic-oblong to lanceolate, apex acuminate, base acute to obtuse, glabrous above, puberulent on veins below, with conspicuous brown or black pellucid glands. Venation with 4–7 pairs of secondary veins arising along the length of the midrib, loop-connecting to apex. Petioles 3–15 mm long, puberulent. Prophylls 6–15 (–20) mm long, glabrous to minutely pubescent. Inflorescences 4–8 (–11) cm long,

Fig. 2 A: *P. guanacostense*, habit; a: prophyll; b: bract and fruit. B: *P. trigonum*, habit; c: prophyll; d: bract and fruit. C: *P. rupununianum*, habit; e: prophyll; f: bract and fruit; g: leaf section.

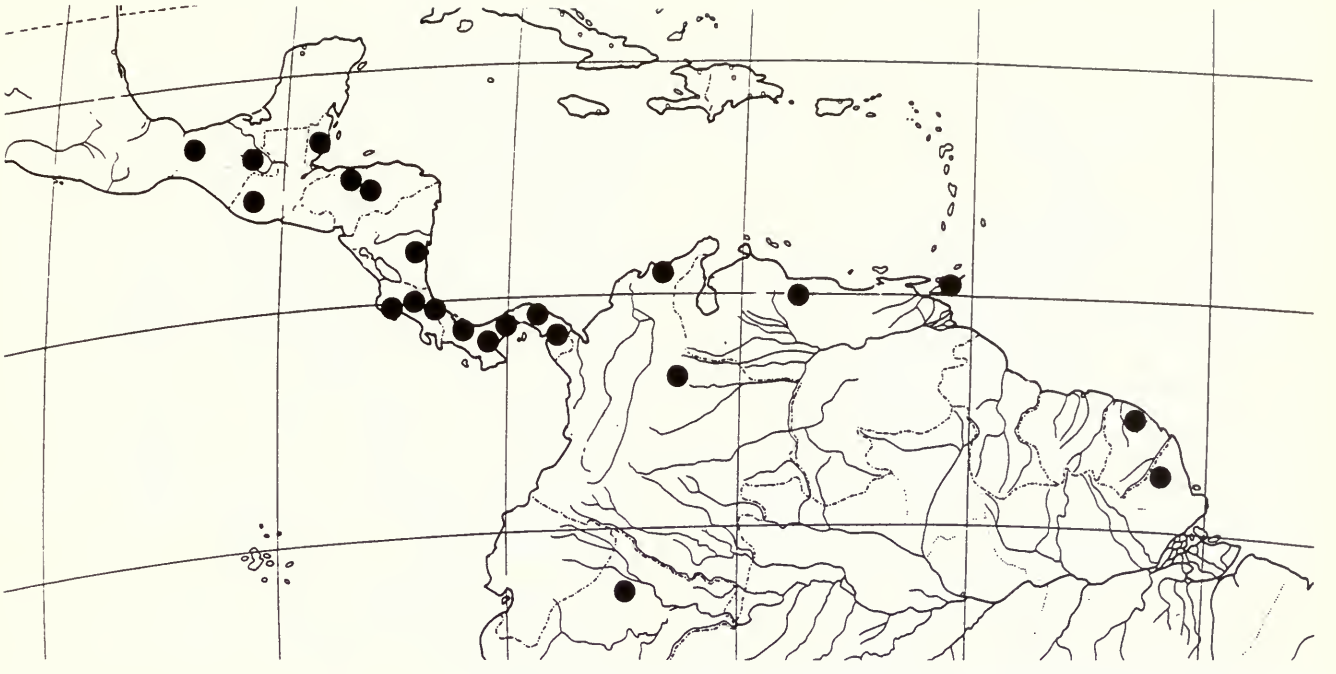

Fig. 3 Distribution of *P. trigonum*.

becoming pendulous in fruit; peduncles 6–15 mm long, puberulent. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, triangular, sparsely pubescent. Fruit obovoid, 1–1.5 (–2) mm wide, trigonous, shortly pubescent or granular, glandular on upper surface; stigmas 3, in small depression.

Growing in shade at forest edges, trail sides, and along banks of streams; 0–1200 m.

DISTRIBUTION Mexico–Brazil. Fig. 3.

Mexico, Oaxaca: *Chavelas & Perez* 294 (MEXU); Chiapas: *Gilly & Xolocotzi* 189 (MEXU). **Guatemala**, Quetzaltenango: *Croat & Hannon* 63423 (BM, MO). **Honduras**, Morazan: *Martinez* 1 (BM). **Nicaragua**, Zelaya: *Vincelli* 157 (MO). **Costa Rica**, Alajuela: *Liesner* 14115 (MO); Heredia: *Opler* 92 (F); Limón: *Burger & Antonio* 11228 (F); Puntarenas: *Liesner* 1901 (MO). **Panama**, Bocas del Toro: *Kirkbride & Duke* 773 (NY); Coclé: *Hammel* 4791 (MO); Colon: *Kennedy* 2787 (MO); Darien: *Croat* 37710 (MO); Panama: *Croat* 17308 (MO); Perlas, San José Is.: *Johnston* 1215 (BM); San Blas: *Duke* 14875 (MO); Veraguas: *Nee* 11269 (MO). **West Indies**, Trinidad: *Broadway* 6206 (BM). **Colombia**, Santa Marta: *Smith* 2736 (K, NY); Santander: *Killip & Smith* 14875 (BM, US). **Venezuela**, Aragua: *Croat* 54482 (BM,MO). **French Guiana**, Cayenne: *de Granville* 6561 (K). **Peru**, Loreto: *Jones* 7175 (ILL). **Brazil**, Amapa, Rio Oiapoque: *Irwin* et al. 47222 (K).

Piper trigonum occurs in the deep shade of swamp forest, lowland rain-forest, and secondary vegetation. Its leaf shape, venation, and the presence of pellucid glands on the stems, leaves, and fruits show an affinity with *P. atroglandulosum*. *Piper trigonum* can be distinguished by its pubescent young stems, sparsely pubescent floral bracts, and widely triangular, glandular, pubescent, or granular fruits. Specimens from Trinidad are generally less pubescent than those on the mainland, and the fruits have a less pronounced granular surface.

23. **Piper rupununianum** Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 303 (1950). Type: Guyana, Tumatumari, *Gleason* 107 (NY-holotype; K!-isotype).
Fig. 2C, e, f, g.

Spreading shrub or subshrub, 1–2 m high, stems glandular. Leaves 14–22 cm long, 4–8 cm wide, oblong-elliptic to lanceolate, glabrous, glossy above, puberulent on veins beneath, with orange or brown glands on both surfaces, apex acute-acuminate, base acute to obtuse. Venation with 3–4 pairs of secondary veins arising from the lower to middle part of midrib, loop-connecting to apex. Petioles 5–10 mm long. Prophylls 5–15 mm long, glabrous, glandular. Inflorescences 8–11 cm long, erect, sometimes pendulous in fruit; peduncles 15–30 mm long, slender. Anthers 0.2–0.3 mm long. Floral bracts 0.8–1 mm wide, triangular, densely yellow-ciliate, with dark, glabrous centre. Fruit obovoid, 1–1.5 mm wide, trigonous, glandular, slightly granular; stigmas 3, sessile.

Clearings, damp places, secondary mixed forest, and shady rocky areas; 0–400 m.

DISTRIBUTION. Guyana. Fig. 4.

Guyana, Aremoo Creek: *Bartlett* 8408 (K); Oko Creek: *Tutin* 318 (BM); Mabaruma: *Forest Dept.* F2509 (K); Potars district: *Whitton* 102 (K).

This small, spreading shrub is apparently confined to Guyana. It can be recognized by its large glossy leaves with orange or brown pellucid glands, and inflorescences with long peduncles. The floral bracts are similar to those of *P. atroglandulosum* or

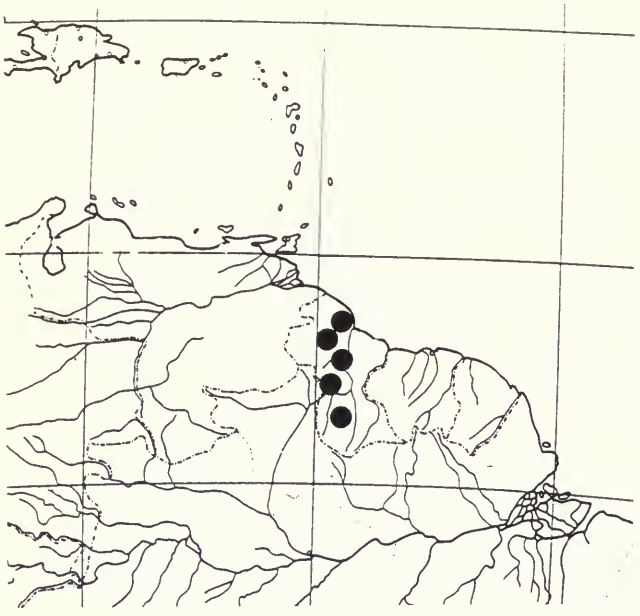

Fig. 4 Distribution of *P. rupununianum*.

P. divaricatum, with yellow-ciliate margins and dark centres. The glandular, granular fruits are similar to those of *P. trigonum*.

24. **Piper atroglandulosum** Tebbs, **nom. nov.**
Fig. 5A, a, b, c.

P. obovatum Ruiz López & Pavón, *Fl. peruv.* **1**: 36, tab. 53 (1798), non M. Vahl, *Eclog. amer.* **1**: 5 (1796) (Art. 64.1). Type: Peru, Huanuco, Cochero & Chinchao, *Ruiz López & Pavón* s.n. (B-holotype; M!-photograph).
Schilleria obovata Kunth in *Linnaea* **13**: 686 (1839).
Artanthe obovata (Kunth) Miq., *Syst. piperac.*: 508 (1844).

Shrub 1–2 m high, stems glabrous, rarely sparsely pubescent, copiously black- or brown-glandular. Leaves 9–14 cm long, 3–6 cm wide, oblanceolate to elliptic, both surfaces with dark glands, upper surface glossy, apex narrowly long-acuminate, base cuneate. Venation with 5–9 pairs of veins arising along the length of the midrib and curving towards apex. Petioles 5–12 (–15) mm long. Prophylls 1–2.5 cm long, glandular. Inflorescences 3–8 cm long, 4–5 mm wide, curving in fruit; peduncle 6–10 mm long. Anthers 0.2–0.4 mm long. Floral bracts 1 mm wide, triangular, densely pale yellowish-ciliate. Fruit obovoid, 1–2 mm wide, trigonous, glabrous, glandular; stigmas 3.

Edges of forest; 0–800 m.

DISTRIBUTION. Colombia–Bolivia. Fig. 6.

Colombia, El Meta: *Haught* 2759 (BM, US). **Peru**, Casapi: *Mathews* 1692 (K). **Ecuador**, Napo-Pastaza: *Mexia* 7230 (BM, US). **Bolivia**, Tumupasa: *Williams* 465 (K).

This species is closely related to *P. divaricatum*, with similar leaf shape, type of venation, and prominent glands. It differs from that species mainly by its obovate leaves with long narrow apices, dark glands, much smaller prophyll and western Andean distribution. It is also similar to *P. heterophyllum* Ruiz López & Pavón, but the latter has a short style and round fruit. However, these species can be difficult to segregate in dried herbarium specimens without mature inflorescences.

Piper obovatum Ruiz López & Pavón is a later homonym of *Piper obovatum* M. Vahl, published two years earlier in 1796, and is hence illegitimate. *Piper obovatum* M. Vahl, however, was placed in the genus *Peperomia* by A. Dietrich (1831) in the synonymy of *Peperomia obversa* (M. Vahl) A. Dietr. (basionym *Piper obversum* M. Vahl, *Enum. pl.* **1**: 354 (1804)). Casimir de Candolle (1902) correctly placed *Peperomia obversa* into synonymy under *Peperomia obovata* (M. Vahl) C. DC. as the earliest published name, leaving the Ruiz López & Pavón species without a legitimate name. Unusually for this genus, no later name has been found that could be adopted as a name for *Piper obovatum* Ruiz López & Pavón. It was thought at first that it should be placed in *P. divaricatum*, but its distinctive leaf shape, western distribution, and different habitat have prevented this; therefore, it has been necessary to provide a new name for this species.

25. **Piper divaricatum** G. Meyer, *Prim. fl. esseq.*: 15 (1818). Type: Surinam, *Weigelt* s.n. (W-holotype; SP!-photograph).
Fig. 5B, d, e, f.

P. nitidum M. Vahl, *Enum. pl.* **1**: 314 (1804), non Swartz (1788) (Art. 64.1). Type: *Vahl* s.n. (C-holotype).
P. colubrinum Link, *Jb. Gewächsk.* **1** (3): 61 (1820), nom. nud. (Art. 32.1).
P. impunctatum Link, *Jb. Gewächsk.* **1** (3): 62 (1820). Type: Brazil, *Willdenow* 645 (B-holotype).
P. crassum Vell. Conc., *Fl. flumin.*: 25, t.59 (1825). Type: Brazil, *Vellozo* s.n. (R-holotype).
Schilleria colubrina Link ex Kunth in *Linnaea* **13**: 685 (1839). Type: Brazil meridionali, *Gaudichaud* 86 (G-holotype).
Piper densispicatum Steudel, *Nomencl. bot.* ed. 2, **2**: 340 (1841), nom. nud. (Art. 32.1).
Peltobryon attenuatum Klotzsch ex Miq., *Syst. piperac.*: 371 (1844). Type: Brazil, *Martius* 1209 (K!-isosyntype).
Artanthe colubrina (Link ex Kunth) Miq., *Syst. piperac.*: 512 (1844).
A. glabella Miq., *Syst. piperac.*: 371 (1844). Type: Cayenne, *Poiteau* s.n. (G-holotype).
A. tejucensis Miq., *Syst. piperac.*: 496 (1844). Type: Brazil ad Tejuco, *Vauthier* 481 (G-holotype).
A. adenophylla Miq. in *Linnaea* **20**: 170 (1847). Type: Brazil, Coralfalga, *Pohl* 5026 (W-holotype).
A. colubrina var. *crassifolia* Miq. in *Linnaea* **20**: 170 (1847). Type: Brazil, *Pohl* 53 (W-holotype).
A. subaequalis C. Presl, *Epimel. bot.*: 226 (1849). Type: Brazil, Rio de Janeiro, *Mikan* s.n. (W-holotype).
Piper apiculatum C. DC. in DC., *Prodr.* **16**(1): 273 (1869). Type: Brazil, *Riedel* 71 (K!-isotype).
P. crassifolium (Miq.) C. DC. in DC., *Prodr.* **16**(1): 301 (1869).
P. glabellum (Miq.) C. DC. in DC., *Prodr.* **16**(1): 312 (1869), non Swartz (1788) (Art. 64.1).
P. leiophyllum C. DC. in DC., *Prodr.* **16**(1): 297 (1869). Type: Brazil, Bahia, *Blanchet* 3152 (W-holotype).
P. subaequale (C. Presl) C. DC. in DC., *Prodr.* **16**(1): 371 (1869).
P. tejucense (Miq.) C. DC. in DC., *Prodr.* **16**(1): 287 (1869).
P. glabrilimbum C. DC. in *Verh. bot. Ver. Brandenb.* **47**: 107 (1905). Type: Brazil, Amazonas, *Ule* 47b (B-holotype).
P. belemense C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 458 (1917). Type: Brazil, Belem, *Huber* 145 (G-holotype).

Fig. 5 A: *P. atroglandulosum*, habit; a: prophyll; b: bract and fruit; c: leaf section. B: *P. divaricatum*, habit; d: prophyll; e: bract and fruit; f: leaf section. C: *P. dumosum*, habit; g: prophyll; h: bract and fruit.

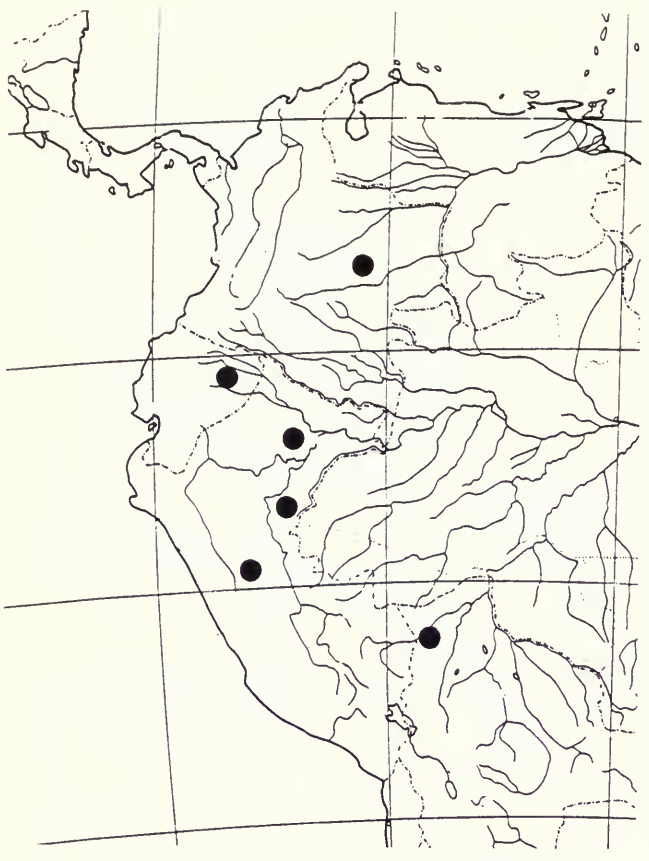

Fig. 6 Distribution of *P. atroglandulosum*.

P. guedesii C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 436 (1917). Type: Brazil, Ilha mexicana, *Guedes* s.n. (G-holotype).

P. oblongilimbum C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 448 (1917). Type: Brazil, Alto Purus, *Huber* 4418 (G-holotype).

P. insipiens Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 224 (1950). Type: Cayenne, *Poiteau* s.n. (G-holotype).

Shrub 1–3 m high, sometimes straggling, stems glabrous, with yellow, red, or brown glands. Leaves 13–18 cm long, 4–7 cm wide, ovate-lanceolate to ovate-elliptic, subcoriaceous, glossy above, glabrous, both surfaces covered with yellow or reddish glands, apex acute, blunt, base ovate to sub-obtuse. Venation with 4–6 pairs of secondary veins arising mostly from the lower to middle part of midrib, loop-connecting to apex. Petioles 10–15 mm long. Prophylls 1–3 cm long, glabrous, glandular. Inflorescences 5–15 cm long, 5–8 mm wide when mature, curving or pendulous in fruit; peduncles 6–12 mm long. Anthers 0.3–0.4 mm long. Floral bracts 0.8–1 mm wide, triangular, fleshy, broadly and densely yellow-white-ciliate. Fruit obovoid, 1–2 mm wide, trigonous, glabrous, glandular; stigmas 3, sessile.

Forest, wet soil along river banks, and in riverine woodlands; 0–300 m.

DISTRIBUTION. Guyana–Brazil. Fig. 7.

Surinam, *Hostmann* 709 (BM). **Guyana**, Demerara River: *Jenman* 4206 (NY); Parika: *Davis* 1967 (K). **Brazil**, Amapa: *Egler & Irwin* 46024A (K); Amazonas: *Prance* et al. 16325 (K); Bahia: *Glocker* 7 (BM); Goiás: *Prance & Silva* 59663 (K); Pará: *Baker* 413 (E); Rondonia: *Cid* et al. 4554 (K); Roraima: *Prance* et al. 11103 (K).

Trelease & Yuncker (1950) placed *Piper nitidum* M. Vahl into synonymy under *P. divaricatum*, without citing type material, although they may have seen it. Yuncker (1972) reduced 16 species of *Piper* to synonymy under *P. divaricatum*, and noted the 'considerable variation in the size, shape and texture of the leaves, and, to some extent, also in the nervation.' *Piper divaricatum* can be recognized by its ovate-lanceolate to ovate-elliptic, glabrous leaves, both surfaces of which are copiously glandular. It is also found in wetter conditions, most frequently along river banks, and its easterly distribution separates it further from *P. atroglandulosum*, which is mostly confined to the western side of the Andes.

26. **Piper dumosum** Rudge, *Pl. Guian.* **1**: 13 (1805). Type: Guiana, *Martin* s.n. (BM!-holotype).
Fig. 5C, g, h.

Shrub or treelet, 1–3 (–4)m high, stems glabrous or with scattered pale hairs 1–1.5 mm long, glandular. Leaves 15–23 cm long, (4.5–) 7–11 cm wide, narrowly to broadly elliptic or oblong-elliptic, upper surface sparsely pubescent, lower surface sparsely to moderately pubescent, copiously red- or black-glandular, apex acute-acuminate, base obtuse or sub-obtuse. Venation with 5–9 pairs of secondary veins arising from along most of the length of the midrib, curving towards apex. Petioles 0.5–1.5 (–2) cm long, glabrous or sparsely pubescent, vaginate at or near base. Prophylls 1–2 cm long, pale, leaf-like, covered in brown or black glands. Inflorescences 5–10 cm long, 3–5 mm wide when mature, yellowish white or brown, usually pendulous; peduncles 5–12 mm long, with black glands. Anthers 0.3–0.4 mm long. Floral bracts 0.5–0.8 mm wide, triangular, shortly yellowish-ciliate. Fruit obovoid, 1–2 mm wide, trigonous, glabrous, glandular; stigmas 3, sessile.

Shady moist places in primary and secondary forest and along track sides; 0–600 m.

DISTRIBUTION. French Guiana to Brazil. Fig. 8.

French Guiana, *Poiteau* s.n. (K). **Guyana**, Pakaraima mts: *Maas* et al. 5603 (K). **Brazil**, Acre: *Prance* et al. 7630 (K); Amapa: *Irwin* et al. 48433 (K); Amazonas: *Lleras* et al. P16615 (K); Para: *Prance & Pennington* 2020 (K); Rondonia: *Prance* et al. 9006 (K).

Piper dumosum can be identified by its moderately pubescent leaves with red or black glands, and the large, rather leaf-like, copiously glandular prophylls.

27. **Piper imberbe** Trel. & Standley in *Fieldiana Bot.* **24** (3): 303 (1952). Type: Guatemala, Izabal, between Escobas & waterfall, *Steyermark* 39857 (F!-holotype).
Fig. 15A, a.

Subshrub, sometimes epiphytic, 0.5–1 m high, stems spreading or decumbent, strongly ridged when dry, glabrous or sometimes minutely puberulent on young growth. Leaves 17–23 cm long, 4.5–9.5 cm wide, lanceolate, peltate, glabrous, sparsely glandular, subcoriaceous, dull green above, paler beneath, narrowing to long acuminate apex; peltate

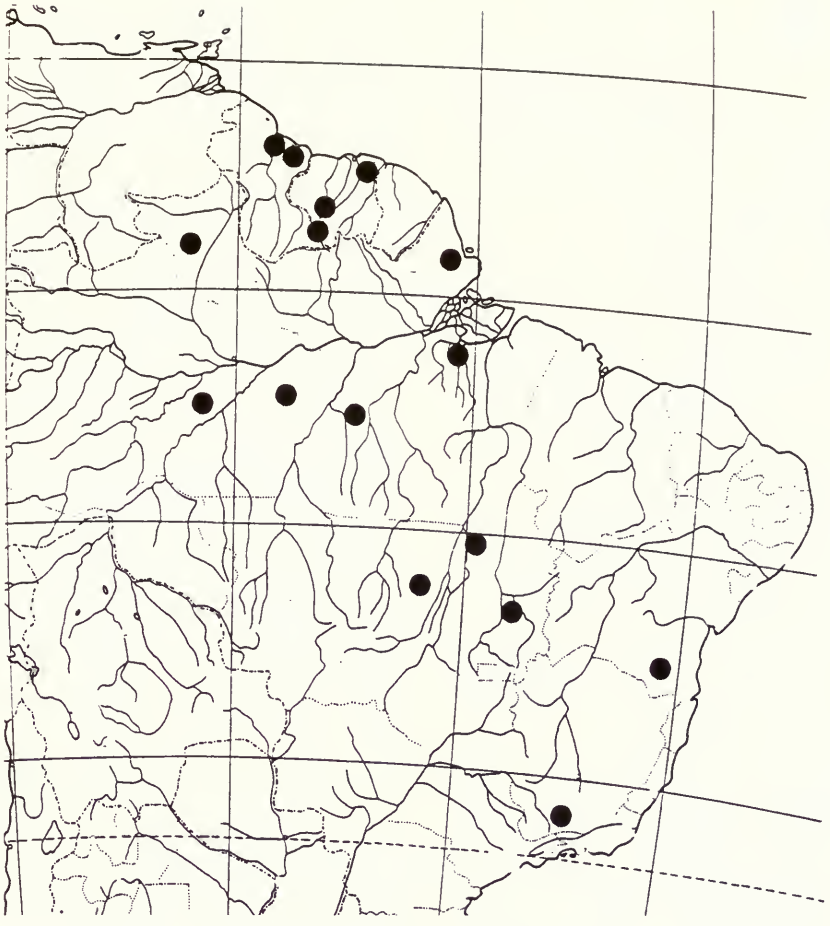

Fig. 7 Distribution of *P. divaricatum*.

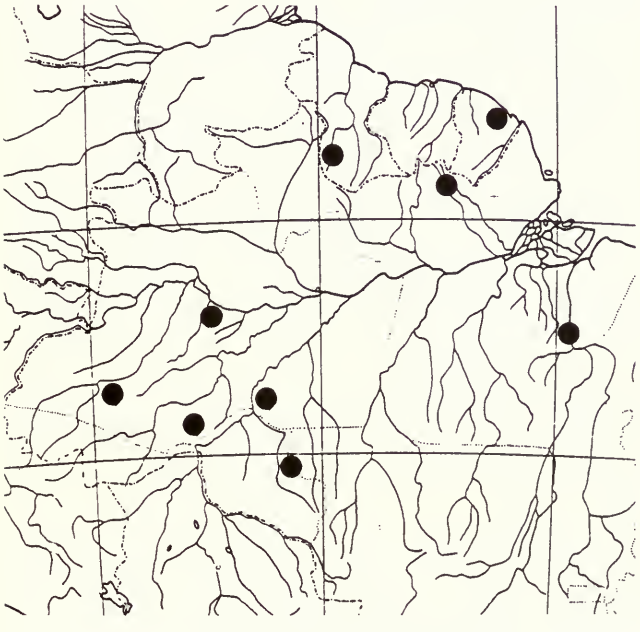

Fig. 8 Distribution of *P. dumosum*.

base round. Venation with 2–3 pairs of secondary veins radiating from petiole attachment, and 4–6 pairs arising along the length of the midrib. Petioles 3–5 cm long. Prophylls 1–3 cm long, narrow. Inflorescences erect, 7–9 cm long; peduncles 10–12 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.4–0.6 mm wide, triangular to orbicular, fleshy, glabrous. Fruit obovoid, 0.7–0.9 mm wide, trigonous, glabrous, apex domed; stigmas 3, linear.

Moist forest; 0–100 m.

DISTRIBUTION. Guatemala, Honduras. Fig. 9.

Guatemala, Izabal: *Steyermark* 39857 (F, NY). **Honduras**, Olancho: *Blackmore & Heath* 2034 (BM).

This distinctive plant has only been collected a few times. It can be distinguished mainly by its diminutive habit and peltate lanceolate leaves.

28. **Piper xylosteoides** (Kunth) Steudel, *Nomencl. bot.* ed. 2, **2**: 344 (1841).
Fig. 11A, a, b, c.

Schilleria xylosteoides Kunth in *Linnaea* **13**: 677 (1839). Type: Brazil, *Sellow* s.n. (K!-isotype).
Artanthe xylosteoides (Kunth) Miq., *Syst. piperac.*: 422 (1844).

Fig. 9 Distribution of *P. imberbe*.

A. concinna Miq. in *Linnaea* **20**: 151 (1847). Type: Brazil, *Pohl* 5032 (W-holotype; SP!-photograph).
Piper concinnum (Miq.) C. DC. in DC., *Prodr.* **16**(1): 328 (1869), non Haworth (1821) (Art. 64.1).
P. pabstii C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 448 (1917). Type: Brazil, Santa Catarina, *Pabst* 408 (B-holotype).
P. concinnatoris Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 33 (1966). Type as for *Artanthe concinna* Miq.

Slender shrub 2–3 m high, stems glabrous. Leaves ovate-elliptic to oblong-elliptic, 7–11 cm long, 2–4 (–5) cm wide, glossy above, glabrous, with scattered pellucid glands, apex acute to acuminate, base acute. Venation with 2 pairs of secondary veins arising from or near the base and curving to apex, and 1–2 pairs from further up the midrib. Petioles 6–10 mm long. Prophylls 6–8 mm long. Inflorescences 3–6.5 cm long, erect; peduncles 5–10 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, triangular-conchiform, fleshy, glabrous. Fruit obovoid, 0.8–1 mm wide, trigonous, apex slightly domed, sometimes with minute style 0.5 mm, glabrous; stigmas 3.

Fig. 10 Distribution of *P. xylosteoides*.

Cool mountain areas; 700–1600 m.

DISTRIBUTION. South-eastern Brazil. Fig. 10.

Brazil, Rio de Janeiro: *Burchell* 6686 (BM).

This species is very similar in leaf-form to *P. urophyllum*, but lacks the distinctive thickening of the leaf-base. The fruits are smaller and less prominent in *P. xylosteoides*.

29. **Piper urophyllum** C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 170 (1897). Type: Costa Rica, Bois dans la vallée du Rio Tuis (bassin du Reventazón), 600 m, *Tonduz* 8159 (G-holotype; M!-isotype).
Fig. 11B, d, e, f, g.

P. sarapiquinum C. DC. in *An. Inst. fís.-geogr. C. Rica.* **9**: 166 (1897). Type: Costa Rica, Hacienda Vieja, bord du Sarapiquí, *Biolley* 7437 (?P-holotype).

Slender, sometimes lax shrub, 1.5–4 m, stems glabrous, often producing roots at nodes. Leaves 7–14 cm long, 2.5–6 cm wide, elliptic, glabrous, greyish green, narrowing abruptly to slender apex 1–2 cm long, base thickened at petiole. Venation with 4–7 pairs of secondary veins arising from along the length of the midrib, curving towards apex. Petioles 5–10 mm long. Prophylls 4–8 (–15) mm long, pale green, apex blunt. Inflorescences 4–8 cm long, pale green; peduncles 1–2 cm long. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, triangular, fleshy, glabrous. Fruit obovoid, 1–2 mm wide, broadly trigonous, with minute style; stigmas 3, linear.

Moist forests, remnant woods, and stream sides; 0–1000 m.

DISTRIBUTION. Nicaragua–Panama. Fig. 12.

Nicaragua, Zelaya: *Pipoly* 3754 (MO, BM). **Costa Rica**, Alajuela: *Lent* 2654 (NY); Cartago: *Liesner* et al. 15287 (US); Guanacaste: *Standley & Valerio* 45913 (US); Heredia: *Opler* 1597 (NY); Limón: *Davidson & Donahue* 8684 (CAS); Puntarenas: *Burger & Stolze* 5525 (MO). **Panama**, San Blas: *Sugden* 513 (K).

The habit of this slender, lax shrub, often rooting at the lower nodes, is similar to that of *P. mikanianum*, although the latter is generally smaller and more spreading. *P. urophyllum* has distinctive leaves that narrow abruptly at the top to form long narrow apices, and bases that are thickened at their attachment to the petiole. This thickening gives the appearance of small 'lips', that dry to a darker colour than the rest of the leaf. When ripe, the fruit is prominent on the inflorescence, and, with the distinctive leaves, makes this species easily recognizable. *Piper subrepens* has similar leaves, but lacks the thickening at the base, and has smaller, less prominent mature fruits. Burger (1971) united *P. sarapiquinum* with *P. urophyllum* and therefore the latter name should be used (Art. 57.2).

30. **Piper subrepens** Trel. in *Ann. Mo. bot. Gdn.* **24**: 187 (1937). Type: Panama, C. Valle Chiquito, Coclé, *Seibert* 504 (MO!-holotype; K!, NY!-isotypes).
Fig. 11C, h, i, j.

Glabrous, nodose shrub, stems glossy. Leaves 4–8 cm long, 2–3.5 cm wide, ovate-lanceolate, upper surface glossy, apex acuminate, base obtuse, symmetrical or slightly asymmetrical. Venation with 3–4 pairs of secondary veins, loop-connecting towards apex. Petioles 7–12 mm long, vaginate to middle, glabrous. Prophylls 3–6 mm long, slender, acute.

Fig. 11 A: *P. xylosteoides*, habit; a: prophyll; b: part of inflorescence; c: bract and fruit. B: *P. urophyllum*, habit; d: prophyll; e: leaf-base; f: part of inflorescence; g: bract and fruit. C: *P. subrepens*, habit; h: prophyll; i: part of inflorescence; j: bract and fruit. D: *P. mikanianum*, habit; k: prophyll; l: part of inflorescence; m: bract and fruit.

Fig. 12 Distribution of *P. urophyllum*.

Inflorescences 2–3 cm long; peduncles 6–10 mm long, glabrous. Anthers 0.2 mm long. Floral bracts 0.5 mm wide, triangular, fleshy, minutely ciliate. Fruit obovoid, 0.5–0.8 mm wide, trigonous, with domed apex; stigmas 3, recurved.

Mountain slopes; 700–800 m.

DISTRIBUTION. Panama. Fig. 13.

There is no record of the height of *P. subrepens*, either in the original description or in collection data. *Piper subrepens* resembles *P. urophyllum* in inflorescence, floral bracts, and fruit structure, although the mature fruits are smaller and less prominent in the former. The leaves are ovate-lanceolate as opposed to elliptic, and do not have the abruptly narrowed apex and thickened base of *P. urophyllum*. This species is not well represented in herbaria, and only type material has been examined. It is an endemic of Panama, occurring only on the western slope and summit of Cerro Valle Chiquito in Coclé.

31. **Piper mikanianum** (Kunth) Steudel, *Nomencl. bot.* ed. 2, **2**: 342 (1841).
Fig. 11D, k, l, m.

Fig. 13 Distribution of *P. subrepens*.

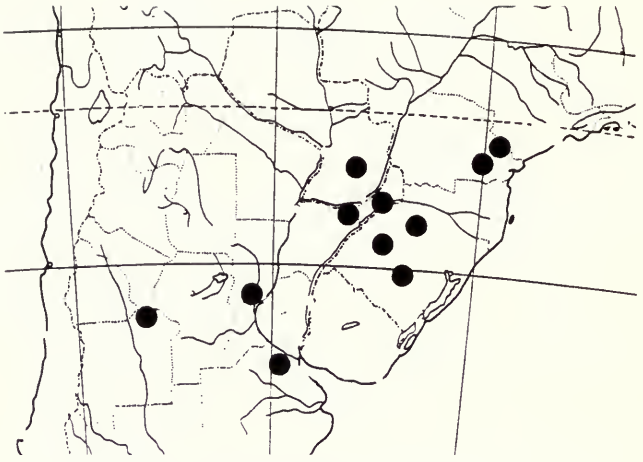

Fig. 14 Distribution of *P. mikanianum*.

Schilleria mikaniana Kunth in *Linnaea* **13**: 719 (1839). Type: Brazil, *Sellow* s.n. (B-holotype; K!-isotype).
Artanthe mikaniana (Kunth) Miq., *Syst. piperac.*: 383 (1844).
Piper parthenium C. DC. in DC., *Prodr.* **16**(1): 330 (1869). Type: Brazil meridionali, *Sellow* s.n. (B-holotype).
P. debile C. DC. in *Bull. Herb. Boissier* **2** (2): 400 (1903). Type: Paraguay, in sylva Pacoba, *Hassler* 4517 (BAF-holotype, photograph!).
P. parthenium var. *pilosius* C. DC. in *Bull. Soc. bot. Genève* II, **6**: 108 (1914). Type: Paraguay, Cordillera de Villa Rica, *Hassler* 8706 (G-holotype).
P. misionesanum C. DC. in *Reprium Spec. nov. Regni veg.* **14**: 395 (1916). Type: Argentina, Santa Ana Missiones, *Hassler* s.n. (BAF-holotype).
P. mikanianum forma *clausum* Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 55 (1966). Type: Brazil, Rio Branco do Sul, Paraná, *Hatschbach* 7261 (Herbario Hatschbach, Curitiba-holotype, photograph!).
P. mikanianum var. *peltatum* Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 54 (1966). Type: Brazil, Minas Gerais, *Regnell* II 256 (S-holotype).

Spreading or decumbent shrub, 0.5–1 m high, stems glabrous to minutely pubescent, rooting at lower nodes. Leaves 6–14 cm long, 3–8 (–11) cm wide, ovate-lanceolate, apex acute-acuminate, glabrous to sparsely pubescent, base obtuse to shallowly or deeply cordate. Venation with 2–3 pairs of secondary veins arising from the base, and 1–2 pairs from further up the midrib. Petioles 0.5–3 (–5) cm long, glabrous to sparsely pubescent. Prophylls 5–15 mm long. Inflorescences 3–6 cm long, fragrant; peduncles 8–20 mm long, glabrous to minutely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.6 mm wide, triangular, fleshy, glabrous or minutely ciliate. Fruit obovoid, 0.8–1 mm wide, trigonous, apex convex, glabrous; stigmas 3, linear.

Margins of woods and gallery forest; 400–1000 m.

DISTRIBUTION. Brazil, Paraguay, Argentina. Fig. 14.

Brazil, Montenegro: *Sehnem* 5055 (B); Gravatai: *Rambo* 42741 (BM); Minas Gerais: *Irwin* et al. 26862 (E); Paraná: *Kummrow* 1305 (MU); Rio Grand do Sul: *Saint-Hilaire* 2796 (K); Santa Catarina: *Smith & Klein* 15519 (B). **Paraguay**, Del

Fig. 15 A: *P. imberbe*, habit; a: bract and fruit. B: *P. carpunya*, habit; b: bract and fruit. C: *P. grande*, habit; c: part of inflorescence; d: bract and fruit.

Guaira: *Montes* 15879 (BM); *Balansa* 2313 (K). **Argentina**, Candelaria: *Montes* 2363 (LIL); Misiones: *Schwindt* 5006 (LIL); Posadas: *Ekman* 1233 (US).

Piper mikanianum is one of the few species of *Piper* to grow in the far south of Latin America, extending well into Argentina. It shares similarities, such as inflorescence, bract, and fruit shape, with *P. urophyllum*. *P. mikanianum* is a sprawling or decumbent shrub, rooting at the lower nodes, a character also shared by *P. urophyllum*. This may also indicate a scandent habit, but there is insufficient evidence available to confirm this.

Piper mikanianum is another species in this section with leaves that range in shape from ovate to cordiform, often on the same plant. The taxa cited above were originally placed into synonymy under *P. mikanianum* by Yuncker (1972).

32. **Piper carpunya** Ruiz López & Pavón, *Fl.peruv.* **1**: 37, t. 63b (1798). Type: Peru, Huánuco, Chinchao et Cuchero, *Pavón* s.n. (MA-holotype, photograph!; F!, BM!-? isotype).
Fig. 15B, b.

Ottonia carpunya (Ruiz López & Pavón) Miq., *Syst. piperac.*: 547 (1844).
O. lessertiana Miq., *Syst. piperac.*: 546 (1844). Type: 'Habit in America meridionali', *Matthews* 1696 (G-holotype; BM!, E!, K!-isotypes).
Carpunya lessertiana (Miq.) C. Presl, *Epimel. bot.*: 229 (1851).
C. peruviana C. Presl, *Epimel. bot.*: 229 (1851). Type as for *P. carpunya*.
Piper lenticellosum C. DC. in *J. Bot., Lond.* **4**: 166 (1866). Type: Colombia, prov. Barbacoas, *Triana* 3 (G-holotype; BM!-isotype).
P. lessertianum (Miq.) C. DC. in DC., *Prodr.* **16**(1): 258 (1869), non C. DC. in *J. Bot., Lond.* **4**: 164 (1866) (Art. 64. 1).
P. cocherense Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **13**: 151 (1936). Type: Peru, Huanuco, *Poeppig* D1354 (W-holotype).
P. subdurum Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 362 (1937). Type: Costa Rica, vicinity of El General, Prov. San José, *Skutch* 2993 (US-holotype; NY!-isotype).

Shrub or small tree 2–3 (–5) m high, stems glabrous, with tubercles. Leaves 9–17 cm long, 5–11 cm wide, ovate-elliptic to oblong-elliptic, coriaceous, glabrous, slightly glossy above, apex acute-acuminate, base round to acute. Venation with 2–5 pairs of secondary veins, arising from lower to middle part of midrib and curving towards the apex, with smaller connecting veins between. Petioles 5–10 mm long, glabrous. Prophylls 1–2.5 cm long, glabrous. Inflorescences erect, 5–10 (–12) cm long; peduncles 5–8 mm long. Anthers 0.3 mm long. Floral bracts 0.7–0.9 mm wide, triangular-cupulate, fleshy, glabrous, or occasionally minutely ciliate. Fruit obovoid, 1 mm wide, upper surface slightly domed, granular or minutely pubescent; stigmas 3, prominent.

Moist woods, remnant rain-forest and scrub, slopes and steep hillsides; 1000–2000 m.

DISTRIBUTION. Costa Rica, Colombia, Ecuador, Peru. Fig. 16.

Costa Rica, Cartago: *Webster & Miller* 12294 (F); Heredia: *Poveda* 955 (F). **Colombia**, Popayan: *Hartweg* 1400 (BM). **Ecuador**, Chimborazo: *Camp* 3525 (K); montis Pululagua: *Andre* 3313 (K). **Peru**, Amazonas: *Young & Eisenberg* 348 (MO, NY); Chachapoyas: *Mathews* 3226 (BM); Chili: *Poeppig* 1354 (BM); Huacafistana: *Sandeman* 4412 (K).

Fig. 16 Distribution of *P. carpunya*.

Piper carpunya can be recognized by its prominently nodose, tuberculate stems, glabrous, coriaceous, pungent-aromatic leaves, short, erect inflorescences, and cupulate bracts. The species is confined to forested areas at high altitudes; only three specimens have been seen from Central America, all collected from mountainous areas in Costa Rica. The first collection is from remnant rain-forest north-east of Paraiso, Cartago Province, at an altitute of 1600 m; the second, originally misidentified as *P. verruculosum* C. DC., is from between San Miguel and Cariblanco, Heredia Province, and does not have altitude or habitat details; the third, the type of *P. subdurum* Trel., was collected from a clearing in the vicinity of El General, San José Province. These collections indicate that *P. carpunya* is more widespread than was previously thought, and not restricted to northern South America.

33. **Piper grande** M. Vahl, *Eclog. amer.*, fasc. **2**: 3, t. 11 (1798). Type: New Granada, Santa Martha, *Von Rohr* 46—labelled as *Piper coriaceum* (C!-holotype; BM!-?isotype).
Fig. 15C, c, d.

P. grandifolium Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 46 (1816). Type: Colombia, montis Quindiu, *Humboldt & Bonpland* s.n. (P-holotype).
P. riparium Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 48 (1816). Type: Colombia, fluminis Magdalenae, *Humboldt & Bonpland* s.n. (P-holotype).

Schilleria riparia (Kunth) Kunth in *Linnaea* **13**: 707 (1839).
S. grandifolia (Kunth) Kunth in *Linnaea* **13**: 709 (1839).
Artanthe grandifolia (Kunth) Miq., *Syst. piperac.*: 408 (1844).
A. riparia (Kunth) Miq., *Syst. piperac.*: 409 (1844).
Piper borucanum C. DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 219 (1892). Type: Costa Rica, forêts près de Boruca, *Pittier* 3609 (G!-holotype).
P. pseudo-variabile Trel. in *Contr. U.S. natn. Herb.* **26**: 23 (1927). Type: Panama, Loma de la Gloria, *Pittier* 3845 (US-holotype, photograph!).
P. pseudo-variabile var. *collium* Trel. in *Contr. U.S. natn. Herb.* **26**: 23 (1927). Type: Panama, Rio Tapla, *Standley* 26130 (US-holotype, photograph!).
P. pseudo-variabile var. *pachypus* Trel. in *Contr. U.S. natn. Herb.* **26**: 24 (1927). Type: Panama, between Frijoles & Monte Lirio, *Killip* 12145 (US-holotype, photograph!).
P. cercidiphyllum Trel. in *Contr. U.S. natn. Herb.* **26**: 146 (1929). Type: Costa Rica, near Tilarán, Guanacaste, *Standley & Valerio* 46110 (US-holotype).
P. subvariabile Trel. in *Contr. U.S. natn. Herb.* **26**: 145 (1929). Type: Costa Rica, near Tilarán, Guanacaste, *Standley & Valerio* 44970 (US-holotype).
P. marmoreum Trel. in *Ann. Mo. bot. Gdn* **24**: 186 (1937). Type: Panama, vicinity of Arenoso, *Seibert* 622 (MO!-holotype; K!, Y!-isotypes).
P. spissinervium Trel. fide Bro. Tomás Alberto in Colegio de San José, Medellín, Colombia Publ. 53–70, p. 18 (1942), nom. nud. (Art. 32.1).

Shrub or small tree 1–3 m high, stems glabrous. Leaves 12–28 cm long, 8–17 cm wide, broadly elliptic to ovate-elliptic, slightly asymmetric, glabrous, apex acuminate, base sometimes slightly cordate. Venation with 4–9 pairs of secondary veins arising along the length of the midrib, those from or near the base ascending more sharply than the rest. Petioles 1–5 cm long. Prophylls 1–3 cm long, glabrous. Inflorescences 8–15 cm long; peduncles 6–15 mm long, glabrous. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, oblong-triangular, fleshy, umbonate, minutely ciliate. Fruit obovoid, 0.8–1 mm wide, trigonous to orbicular, glabrous, covered by bracts; stigmas 3, sessile.

Moist forest, edges of roads, trails and stream sides; 0–1000m.

DISTRIBUTION. Nicaragua to Colombia. Fig. 17.

Nicaragua, *Bunting & Licht* 381 (NY). **Costa Rica**, Puntarenas: *Williams* et al. 24213 (MO). **Panama**, Canal Zone: *Croat* 4380 (MO); Coclé: *Allen* 2001 (MO); Colon: *Dodge* et al. 16924 (MO); Darien: *Duke* 14168 (BM); Panama: *Garwood & Tebbs* 1932A (BM); San Blas: *Duke* 8578 (MO); Veraguas: *Antonio* 2315 (MO, BM).

This species is characterised by its distinctive pale inflorescence with fleshy, umbonate bracts. These conceal the developing fruit, a feature that occurs to a lesser extent in other species in this section, such as *Piper veraguense*. However, even in early stages of development, the floral bracts of *P. grande* are distinctive in their structure. *P.grande* is a common species, often found growing in open areas of secondary forest.

Several species have been synonymised here by previous authors, notably Trelease & Yuncker (1950), the types of which have not been seen by the present author. There seems no reason to dispute this synonymy, however, as the original descriptions compare well with that of *P. grande*.

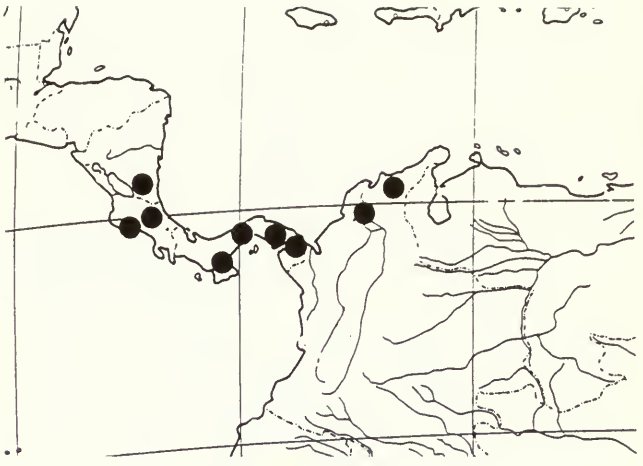

Fig. 17 Distribution of *P. grande*.

34. **Piper lepturum** (Kunth) C. DC. in DC., *Prodr.* **16**(1): 320 (1869).
Fig. 18A, a.

Schilleria leptura Kunth in *Linnaea* **13**: 679 (1839). Type: Brazil, Rio de Janeiro, *Gaudichaud* s.n. (?B-holotype).
S. jussiaeana Kunth in *Linnaea* **13**: 680 (1839). Type: Brazil, Serra d'Estrella. *Luschnath* 292 (B-holotype; SP!-photograph).
Piper jussiaeanum Kunth in *Linnaea* **13**: 680 (1839)—as synonym (Art. 34.1).
Artanthe jussiaeana (Kunth) Miq., *Syst. piperac.*: 420 (1844).
A. leptura (Kunth) Miq., *Syst. piperac.*: 523 (1844).
A. meyeniana Klotzsch ex Miq., *Syst. piperac.*: 524 (1844). Type: Brazil, Rio de Janeiro, *Gaudichaud* s.n. (B-holotype).
A. denudans Miq. in *Linnaea* **20**: 172 (1847). Type: Brazil, monte Corcovado, *Pohl* 4778, 5028 (W-syntypes).
Piper fuscum C. DC. in DC., *Prodr.* **16** (1): 319 (1869). Type: Brazil, *Riedel* 291 (LE).
P. denudans (Miq.) C. DC. in DC., *Prodr.* **16** (1): 324 (1869).
P. denudans var. *angustifolium* C. DC. in DC., *Prodr.* **16** (1): 324 (1869). Type: Brazil, Corcovado, *Pohl* 5028 (W-holotype).
P. dupasquieri C. DC. in *Linnaea* **37**: 361 (1872). Type: Brazil, *Dupasquier* s.n. (G-holotype).
P. glaziovii C. DC. in *Annu. Conserv. Jard. bot. Genève* **2**: 265 (1898). Type: Brazil, Rio de Janeiro. *Glaziou* 7848 (G-holotype).
P. sievekingii C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 435 (1917). Type: ?
P. lepturum var. *angustifolium* (C. DC.) Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 103 (1966).

Shrub 2–3 m high, stems glabrous, glandular. Leaves 11–20 cm long, 3–5 cm wide, lanceolate to oblong-lanceolate, glabrous, with brown or black glands on both surfaces; apex long-acuminate, base obtuse or round. Venation with 1–2 pairs of secondary veins arising steeply from or near the base, and 4–6 pairs arising along the length of the midrib, ascending steeply to apex. Petioles 10–25 mm long, glabrous. Prophylls 8–14 mm long, narrow, apex blunt. Inflorescences 6–10 cm long; peduncles 5–15 mm long, glabrous. Anthers 0.2–0.3 mm

Floral bracts 0.6–0.8 mm wide, triangular-cucullate,

Fig. 18 A: *P. lepturum*, habit; a: bract and fruit. B: *P. aequale*, habit; b: bract and fruit; c: fruit. C: *P. verruculosum*, habit; d: bract and fruit.

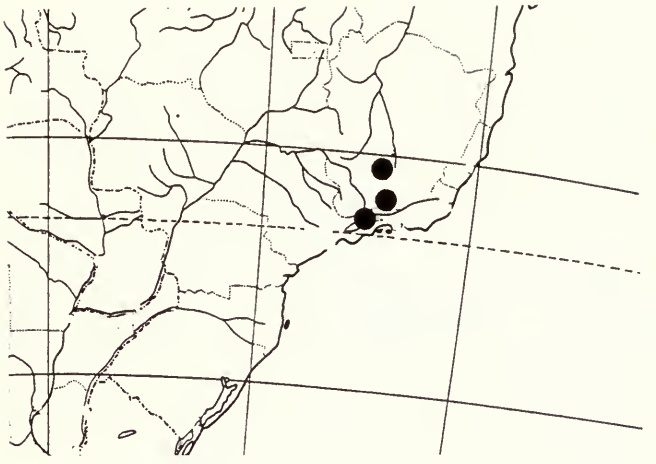

Fig. 19 Distribution of *P. lepturum*.

fleshy, glabrous or minutely ciliate. Fruit obovoid, 1 mm wide, glabrous, glandular, with rounded apex; stigmas 3, linear.

Forest; 0–500 m.

DISTRIBUTION. Brazil. Fig. 19.

Brazil, unlocalized: *Bowie & Cunningham* s.n. 1814–17 (BM); *Sellow* 8 (BM); *Sellow* 137 (BM).

Piper lepturum has similarly shaped leaves to *P. aequale*, but can be distinguished by its glandular stems and leaves, and steeply ascending secondary veins. The floral bracts are smaller, and the fruits have a glandular surface. The names cited above were first placed into synonymy under *P. lepturum* by Yuncker (1972). Although not all of the types of these taxa have been examined for this study, the original descriptions agree with that of *P. lepturum*.

35. **Piper aequale** M. Vahl, *Eclog. amer.* **1**: 4, pl. 3 (1796). Type: Montserrat, *Ryan* s.n. (C!-holotype; BM!-isotype). Fig. 18B, b, c.

P. caripense Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 48 (1816). Type: Caripense Prov. Cumanae, *Humboldt & Bonpland* s.n. (P-holotype).

P. costaricense C. DC. in DC., *Prodr.* **16**(1): 328 (1869). Type: Costa Rica, *Hoffmann* 678 (B-holotype).

P. micranthera C. DC. in *Linnaea* **37**: 354 (1872). Type: Costa Rica, *Oersted* 877 (C!-holotype).

P. donnell-smithii C. DC. ex J.D. Smith, *Enum. pl. guatem.* **2**: 95 (1891). Type: Guatemala, Pansamala, *Tuerkheim* 975 (US?-holotype; NY!-isotype).

P. cabagranum C. DC. in *An. Inst. fís.-geogr. C. Rica.* **9**: 173 (1897). Type: Costa Rica, forêts de Cabagra, *Pittier* 6528 (G-holotype; MO!- photograph).

P. johnstoni C. DC. in *Proc. Am. Acad. Arts Sci.* **40**: 685 (1905). Type: Venezuela: Isla Margarita, Juan Griego Trail, *Johnston* 19 (MO!- holotype; K!-isotype).

P. aequale var. *elliptico-lanceolatum* C. DC. in *Bot. Gaz.* **70**: 171 (1920). Type: Costa Rica, San Ramon, *Pittier* 14185, 14186 (US-syntypes, photograph!).

P. chiriquinum C. DC. in *Smithson. misc. Collns* **71**: 2 (1920). Type: Panama, El Bocquete, *Pittier* 2930 (US-holotype).

P. tenuispicum C. DC. in *Bot. Gaz.* **70**: 170 (1920). Type: Costa Rica, *Tonduz* 13187 (G-holotype; MO!-photograph).

P. pablense Trel. in *Contr. U.S. natn. Herb.* **26**: 23 (1927). Type: Costa Rica, San Pablo de Tarrazu, *Jimenez* 1094 (US-holotype; NY!-isotype).

P. caeruleifolium Trel. in *Contr. U.S. natn. Herb.* **26**: 145 (1929). Type: Costa Rica, Quebrada Serena near Tilarán, *Standley & Valerio* 46134 (US-holotype).

P. concinnifolium Trel. in *Contr. U.S. natn. Herb.* **26**: 167 (1929). Type: Costa Rica, Colinas de Piedades, *Brenes* 14194 (US-holotype).

P. oppressum Trel. in *Contr. U.S. natn. Herb.* **26**: 161 (1929). Type: Costa Rica, Nicoya Peninsula, *Cook & Doyle* 697 (US-holotype, photograph!).

P. seductum Trel. in *Contr. U.S. natn. Herb.* **26**: 135 (1929). Type: Costa Rica, Madre de Dios (Atlantique), *Pittier* 10308 (US-holotype, photograph!).

P. atrichopus Trel. in *J. Wash. Acad. Sci.* **19**: 330 (1929). Type: Honduras, Atlántida, *Standley* 54594 (F-holotype; ILL!-isotype).

P. colemanense Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 337 (1937). Type: Costa Rica, *Dodge & Goerger* 9580 (MO!-holotype).

P. crispans Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 339 (1937). Type: Costa Rica, vicinity of San Ramon, Alajuela, *Brenes* 5236 (F-holotype; NY!-isotype).

P. rubripes Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 358 (1937). Type: Costa Rica, Cerro San José de Libano, *Dodge, Hanckel & Thomas* 6382 (GH-holotype; F!-isotype).

P. epilosipes Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **17**: 344 (1938). Type: Honduras, *Yuncker* et al. 6296 (ILL-holotype; MO!-isotype).

P. paso-anchoense Trel. in *Ann. Mo. bot. Gdn* **27**: 295 (1940). Type: Panama, *Allen* 1579 (ILL-holotype; MO!, NY!-isotypes).

P. jericoense Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 397 (1950). Type: Colombia, *Alejandro* 2730 (US!-holotype).

P. perlasense Yuncker in *Ann. Mo. bot. Gdn* **37**: 67 (1950). Type: Panama, San José Island, *Johnston* 1215 (ILL-holotype; MO!-isotype).

P. cheyennense Trel. & Standley in *Fieldiana Bot.* **24**: 292 (1952). Type: Guatemala, *Steyermark* 39154 (F!-holotype).

P. frioense Standley & Steyerm. in *Fieldiana Bot.* **24**: 299 (1952). Type: Guatemala, *Standley* 90328 (F!-holotype).

Shrub 1–3 (–5) m high, stems glabrous or sometimes minutely puberulent. Leaves 6–20 cm long, 2–9 cm wide, narrowly elliptic, apex acuminate, base acute, equally attached to petiole. Venation with 2–8 pairs of veins arising from along the length of the midrib, 2–3 prominent pairs arising from or near the base. Petioles 6–15 cm long. Prophylls 10–15 mm long, slender, glabrous. Inflorescences erect, pale, 5–10 cm long; peduncles 5–12 mm long, glabrous. Anthers 0.1–0.3 mm long. Floral bracts 0.8–1 mm wide, triangular, fleshy, glabrous or minutely ciliate. Fruit obovoid, 0.8–1 mm wide, trigonous, rounded at apex, glabrous; stigmas 3.

Moist forests, wet ravines, and shaded sides of roads and tracks; 0–2000m.

DISTRIBUTION. Southern Mexico–South America. Fig. 20.

Mexico, Chiapas: *Breedlove & McClintock* 34184 (MO); Tabasco: *Cowan* et al. 2850 (MEXU). **Belize**, Rio Grande: *Schipp* S-452 (BM). **Guatemala**, Alta Verapaz: *Molina* 12163

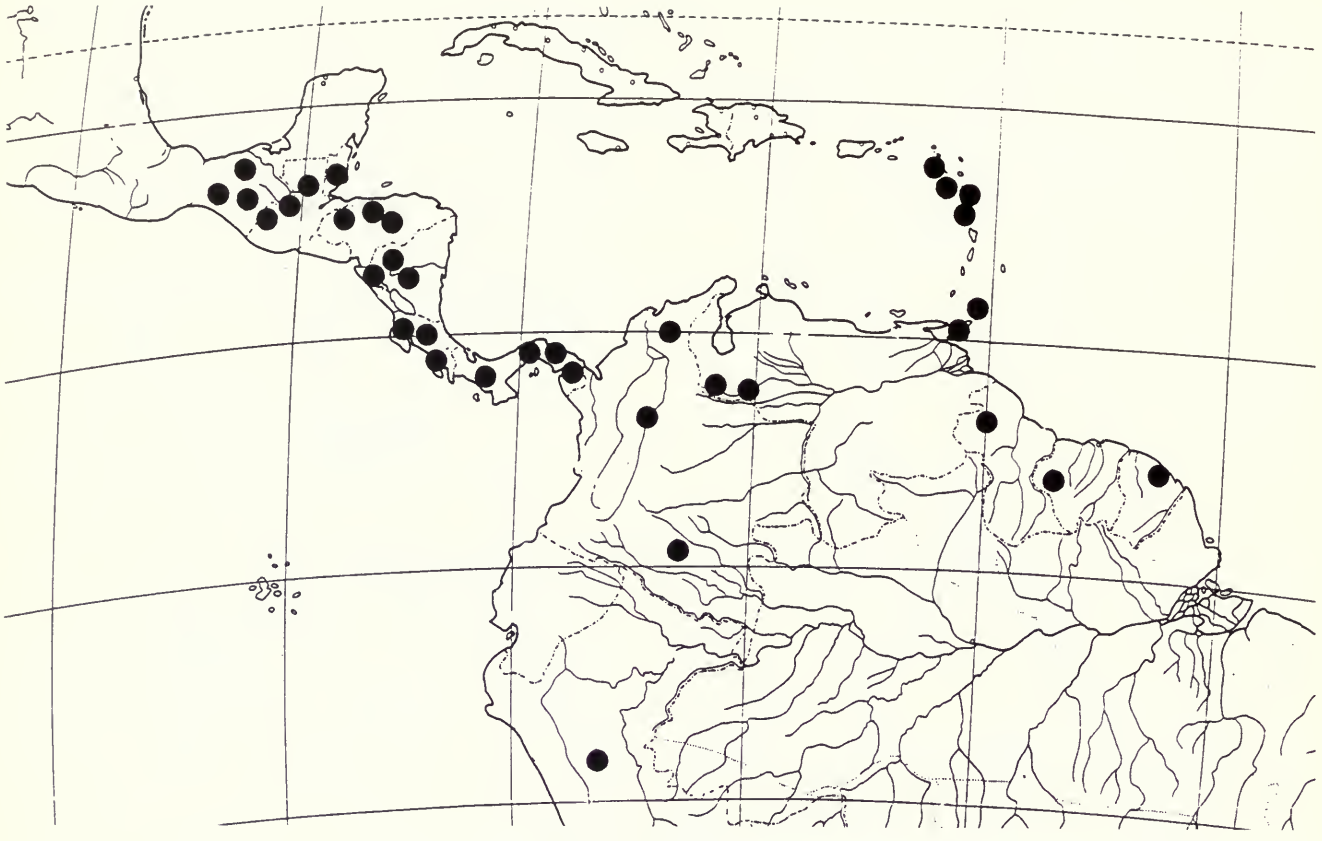

Fig. 20 Distribution of *P. aequale*.

(F, NY); Izabal: *Jones & Facey* 3249 (F); Petén: *Ortiz* 2100 (MO). **Honduras**, Atlantida: *Standley* 56757 (F); Puerto Sierra: *Wilson* 601 (NY). **Nicaragua**, Jinotega: *Standley* 10709 (F); Matagalpa: *Williams* et al. 24813 (F). **Costa Rica**, Alajuela: *Smith* 1848 (NY); Cartago: *Skutch* 4598 (NY); Heredia: *Opler* 729 (MO); Puntarenas: *Croat* 26682 (MO); San José: *Skutch* 4774 (NY). **Panama**, Bocas del Toro: *Kirkbride & Duke* 768 (NY); Canal Zone: *Mori* 7939 (MO); Chiriquí: *Correa & Lazor* 1443 (MO); Coclé: *Nee & Dwyer* 9145 (MO); Darien: *Duke* 14172 (MO); Panama: *Gentry* 6126 (MO); San José Island: *Johnston* 134 (MO); Veraguas: *Croat* 27547 (MO). **Colombia**, Antioquia: *Ewan* 15812 (BM); Magdalena: *Jaramillo* et al. 5214 (B); Santa Marta: *Smith* 1231 (BM). **Venezuela**, Apuré: *Davidse & Gonzalez* 21879 (MO); Carabobo: *Steyermark* 94315 (K). **Surinam**, Juliana Top: *Irwin* et al. 54610 (K); **French Guiana**, Cayenne: *Granville* 6547 (K). **Guyana**, Marudi Hills: *Stoffers* et al. 224 (K). **Brazil**, Amazonas: *Pipoly* et al. 6930 (K); Minaes Geraes: *Mexia* 4666 (B). **West Indies**, Dominica: *Whitefoord* 5625 (BM); Guadeloupe: *Proctor* 20020 (BM); Montserrat: *Howard* 15165 (BM); St Kitts: *Proctor* 19243 (BM); St Lucia: *Proctor* 18162 (BM); Tobago: *Broadway* 4272 (BM); Trinidad: *Broadway* 5804 (BM).

It is possible for the leaves of *Piper aequale* to be confused with those of *P. schiedeanum*, which may also be elliptic-lanceolate in shape. However, the leaf-bases of *P. schiedeanum* are round rather than acute or cuneate as in *P. aequale*. While *P. schiedeanum* often has elliptic, ovate or cordiform leaves on the same plant, the leaves of *P. aequale* are generally uniform in shape. Furthermore, *P. aequale* has a short, slender, acute prophyll, which often dries to a dark brown, while that of *P. schiedeanum* is usually oblong with a blunt tip, and remains pale green on drying. The floral bracts of *P. aequale* do not obscure the young fruits.

36. **Piper verruculosum** C. DC. in *J. Bot., Lond.* **4**: 215 (1866). Type: Costa Rica, Candelaria, *Hoffmann* 8 (B-holotype).
Fig. 18C, d.

P. nudicaule C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 162 (1897). Type: Costa Rica, forêts de Tablazo, *Pittier* 7922 (G-holotype; F!-photograph).
P. carnosicaule Trel. in *Contr. U.S. natn. Herb.* **26**: 168 (1929). Type: Costa Rica, El Muñeco, Cartago, *Standley & Valerio* 51050 (US-holotype).
P. zingiberinum Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 370 (1937). Type: Costa Rica, Santa Clara Hills, *Stork* 2594 (ILL-holotype).

Densely branching shrub 1–3 m high, stems glabrous, glandular. Leaves 7–16 (–19) cm long, 2–7 cm wide, obliquely narrowly elliptic, dark green and slightly glossy above, paler beneath, glabrous, with prominent orange or brown pellucid glands, apex acuminate, base unequally obtuse, Venation with 2–3 pairs of secondary veins arising fairly sharply to apex, with cross-veins. Petioles 3–10 mm long. Prophylls 8–16 mm long, narrow, blunt-tipped. Inflorescences erect, 4–11 cm long, narrow; peduncles 5–10mm long. Anthers 0.2–0.3 mm

Fig. 21 Distribution of *P. verruculosum*.

long. Floral bracts 0.3–0.5 mm wide, triangular, fleshy, minutely ciliate. Fruit obovoid, 0.5–0.8 mm wide, trigonous, upper surface granular-pubescent, slightly domed; stigmas 3, slender, recurved.

Shade in cloud forest; 800–2000 m.

DISTRIBUTION. Costa Rica. Fig. 21.

Costa Rica, Guadeloupe de Zarcero, Alajuela: *Smith* H1127 (F); slopes of Volcán Arenal, Alajuela: *Lent* 2888 (MO).

Only found in mountainous regions of Costa Rica, growing in cloud forest. *Piper verruculosum* is similar to *P. aequale*, sharing characters such as fruit and bract shape, and a narrow prophyll. It differs in its somewhat asymmetric leaves with unequally obtuse bases, distinctly glandular stems and leaves, blunt-tipped rather than acute prophyll, and granular-pubescent fruits.

37. **Piper corrugatum** Kuntze, *Revis. gen. pl.* **2**: 565 (1891). Type: Costa Rica, Port Limón, *Kuntze* s.n. (G-holotype).
Fig. 22.

P. nemorense C. DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 222 (1892). Type: Forêts de Juan Vinas, *Pittier* 1849 (G-holotype; US-isotype, photograph!)
P. riparense C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 173 (1897). Type: Costa Rica, forêts des bords du R. Hacum près de Buenas Aires, *Tonduz* 4893 (G-holotype; BM!-isotype).
P. tsakianum C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 174 (1897). Type: Costa Rica, forêts de Tsaki, Talamanca, *Tonduz* 9532 (G-holotype; F!-isotype).
P. partiticuspe Trel. in *Ann. Mo. bot. Gdn* **27**: 294 (1940). Type: Panama, Coclé, *Allen* 1195 (ILL-holotype; MO!-isotype).

Shrub 1.5–3 m, stems glabrous to densely hirsute, with yellowish multicellular hairs, 0.5–1.5 mm long. Leaves 16–34 (–40) cm long, (7–) 10–28 cm wide, asymmetrically narrowly to broadly ovate-lanceolate to cordiform, coriaceous or subcoriaceous, sometimes bullate, upper surface glabrous to sparsely pubescent, lower surface densely pubescent, apex acuminate, base shallowly to deeply, unevenly lobed, lower leaves usually more deeply lobed than upper. Venation with 3–6 secondary veins arising from or near leaf-base and curving towards apex, 1–2 pairs arising from further up midrib, curving upwards. Petioles 3–5 cm long, glabrous to pubescent, vaginate at base. Prophylls 2–5 cm long, apex blunt. Inflorescences erect, 13–22 cm long, 4–5 mm wide; peduncles 1–2.5 cm long. Anthers 0.2–0.4 mm long. Floral bracts 0.2–0.5 mm wide, oblong-triangular, fleshy, upper part slightly protruding, minutely pubescent on lower margins, sometimes covering fruits in early stages. Fruit obovoid, 0.8–1 mm wide, trigonous, glabrous; stigmas 3.

Woods and forest, shaded areas along roads and trails, and steep banks; 0–1200m.

DISTRIBUTION. Nicaragua to Colombia. Fig. 23.

Nicaragua, Bluefields: *Proctor* et al. 27222 (NY). **Costa Rica**, Alajuela: *Burger* et al. 11842 (NY); Cartago: *Lent* 3042 (F); Limón: *Jimenez* 2794 (F); Puntarenas: *Allen* 6038 (F); San José: *Burger & Stolze* 5307 (F); **Panama**, Chiriquí: *Nee* 10662 (MO); Coclé: *Gentry* 7419 (MO); Panama: *Croat* 12156 (MO); Veraguas: *Mori & Kallunki* 5320 (MO). **Colombia**, Cauca: *Alston* 8153 (BM).

Piper corrugatum is closely related to *P. schiedeanum*, with more or less identical inflorescence characters, and glabrous forms can be very difficult to separate from that species. It has been maintained here as a separate species only because the leaf shape is consistently obliquely oblong-cordate, while *P. schiedeanum* has generally symmetrically elliptic, ovate, or cordiform leaves, often together on the same plant. Furthermore, the leaves of *P. corrugatum* are coriaceous or subcoriaceous, occasionally bullate, and sparsely to copiously pubescent. *P. corrugatum* also has similar inflorescences to the peltate-leaved *P. veraguense*.

Piper riparense appears to be a pilose form of *P. corrugatum*, being otherwise identical morphologically. De Candolle mentions this at the end of his original description of *P. riparense*: 'Species *P. nemorense* C. DC. proxima forsan ejus forma longius pilosior et foliis majoribus.' A wide range of specimens from Nicaragua to Panama has been examined, and no other characters can be found to separate these two species satisfactorily. The leaves of the Panamanian specimens tend to be rougher and more bullate, but this again is variable. The more densely pubescent forms of *P. corrugatum* are commonly found between 0 and 1200 m altitude, while glabrous or sparsely pubescent forms occur between 500 and 1700 m.

38. **Piper schiedeanum** Steudel, *Nomencl. bot.* ed. 2, **2**: 343 (1841). Type: Mexico, in sylvis Misantlae, *Schiede* 1102 (BM!-holotype).
Fig. 24.

P. tiliifolia Schldl. & Cham. in *Linnaea* **6**: 352 (1831), non Desv. ex Ham., *Prodr. pl. Ind. occid.*: 4 (1825) (Art. 64.1).
Artanthe benthamiana Miq. in *Lond. J. Bot.* **4**: 447 (1845). Type: Venezuela, Caracas, *Linden* 216 (K!-holotype).
Piper glanduligerum C. DC. in *J. Bot., Lond.* **4**: 215 (1866). Type: Venezuela, Tovar, *Fendler* 1137, 2400 (G-syntypes; K!-isosyntypes).
P. benthamianum (Miq.) C. DC. in DC., *Prodr.* **16**(1): 264 (1869).
P. tenuifolium C. DC. in DC., *Prodr.* **16**(1): 321 (1869). Type: Mexico, *Pavon* s.n. (G-holotype; MO!-photograph).

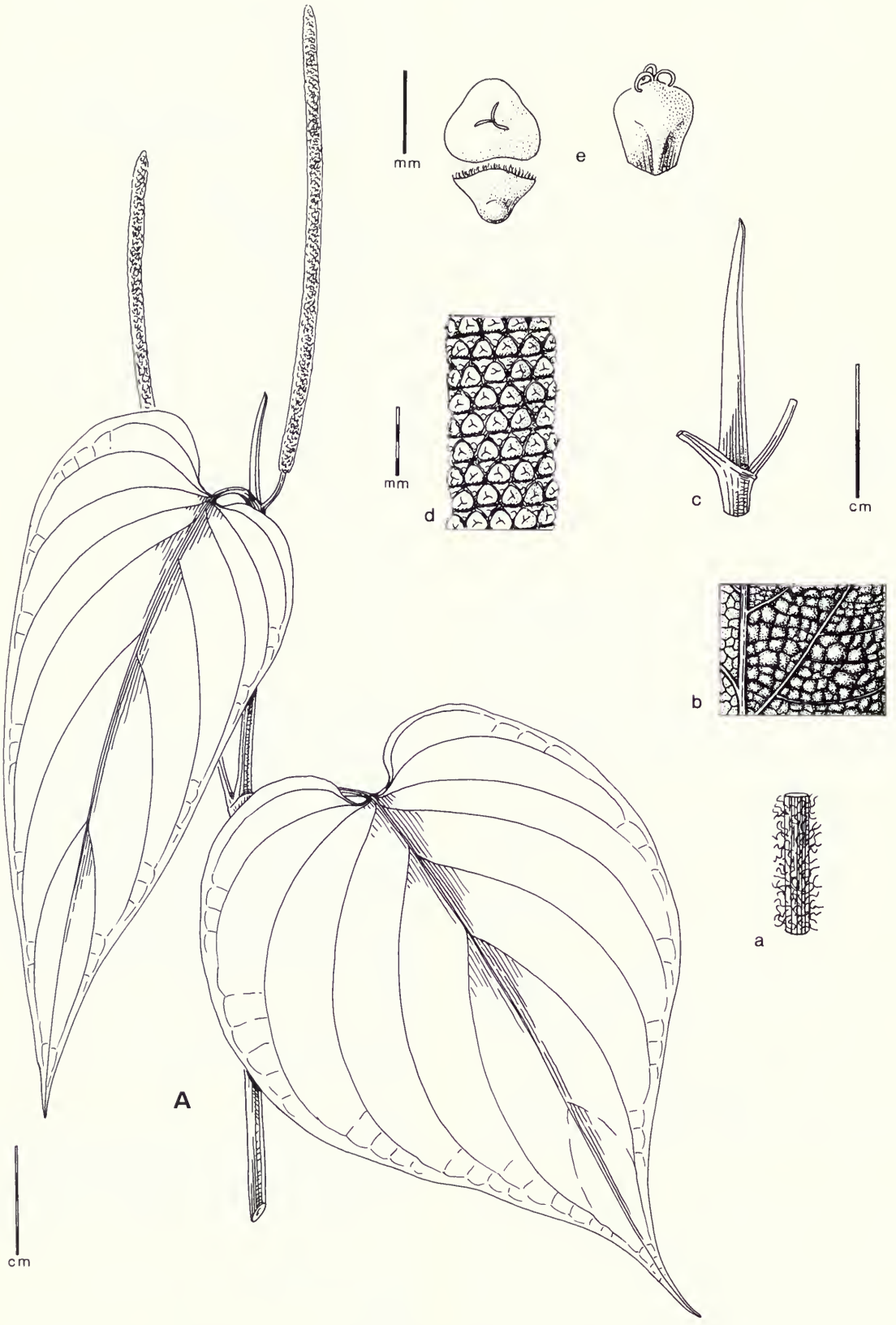

Fig. 22 *P. corrugatum* A: habit; a: pubescent stem; b: rugose leaf surface; c: prophyll; d: part of inflorescence; e: bract and fruit.

Fig. 23 Distribution of *P. corrugatum*.

P. zacuapanum C. DC. in DC., *Prodr.* **16**(1): 330 (1869). Type: Mexico, Zacuapan, *Schiede* 1102 (B-holotype).

P. megalophyllum C. DC. in *Linnaea* **37**: 357 (1872). Type: Mexico, Mirador in sylvis humidis, *Liebmann* 69, 70 (C!-syntypes).

P. megalophyllum var. *connivens* C. DC. in *Linnaea* **37**: 357 (1872). Type: Mexico, Mirador, *Liebmann* 71 (C!-holotype).

P. casimirianum Hemsley, *Biol. cent.-amer., Bot.* **3**: 46 (1882). Type: Nicaragua, Chontales, *Tate* 383 (K!-holotype; BM!-isotype).

P. carrilloanum C. DC. in *Bull. Soc. r. Bot. Belg.* **30** (1): 209 (1892). Type: Costa Rica, Bord de la route a Carrilo, *Pittier* 2525, 2526 (G-syntypes; BM!, K!-isosyntypes of both specimens).

P. vallicolum C. DC. in *Bull. Soc. r. Bot. Belg.* **30** (1): 222 (1891). Type: Costa Rica, bord de la vallée du Rio Jaris près de Pacaca, *Pittier* 3298 (G!-holotype).

P. variabile C. DC. ex J.D. Smith in *Bot. Gaz.* **19**: 259 (1894). Type: Guatemala, Coban, *Tuerckheim* 434 (US-holotype; F!-photograph).

P. paulownifolium C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 173 (1897). Type: Costa Rica, forêts de la Palma, *Pittier* 6739 (G!- holotype).

P. levilimbum Trel. in *J. Wash. Acad. Sci.* **19**: 333 (1929). Type: Honduras, Lancetilla Valley, *Standley* 53483 (F-holotype).

P. omega Trel. in *Contr. U.S. natn. Herb.* **26**: 146 (1929). Type: Costa Rica, La Hondura, *Standley* 37800 (US-holotype, photograph!).

P. middlesexense Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **12**: 103 (1936). Type: Belize, Middlesex, *Schipp* 286 (F-holotype; NY!- isotype).

P. atrichopus var. *arborescens* Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **17**: 347 (1938). Type: Honduras, *Yuncker* et al. 8578 (MO!-holotype).

P. collinum var. *flagellicuspe* Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **17**: 347 (1938). Type: Panama, *Miller* 1773 (MO!-holotype).

P. exigens Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **17**: 345 (1938). Type: Honduras, *Yuncker* et al. 6124 (ILL-holotype; C!, MO!-isotypes).

P. exigens var. *subovatum* Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **17**: 345 (1938). Type: Honduras, *Yuncker* et al. 5997 (ILL-holotype).

P. zarceroense Trel. ex Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 1548, f.9 (1938). Type: Costa Rica, Zarcero, *Smith* H49 (F!-holotype).

P. variabile var. *obtentum* Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **9**: 281 (1940). Type: Honduras, Atlantida, *Yuncker, Koepper & Wagner* 8495 (ILL!-holotype).

P. pergamentifolium Trel. & Standley in *Fieldiana Bot.* **24**(3): 314 (1952). Type: Guatemala, Volcán de Zunil, *Skutch* 876 (F!-holotype).

Shrub or small tree, 2–3 (–5)m high, stems glabrous. Leaves 12–32 cm long, 7–27 cm wide, narrowly to broadly ovate-elliptic to ovate-lanceolate, glabrous or minutely puberulent on veins beneath, apex acuminate, base ovate to deeply cordate. Venation with 4–7 pairs of secondary veins mostly arising from or near the base, curving towards apex, with prominent cross veins. Petioles 2–12 (–20) cm long, glabrous. Prophylls 2–5 cm long, obtuse, glabrous, pale when dry. Inflorescences erect, 10–22 cm long; peduncles 6–20 mm long, glabrous. Anthers 0.2 mm long. Floral bracts 0.4–0.7 mm wide, orbicular to triangular, fleshy, glabrous or minutely ciliate, sometimes covering fruit in early stages. Fruit obovoid, 0.8–1 mm wide, trigonous, glabrous or minutely granular; stigmas 3, sessile.

Disturbed places in moist forest, wooded slopes, roadsides, and trails; 0–1500 m.

DISTRIBUTION. Mexico–Brazil. Fig. 25.

Mexico, Chiapas: *Matuda* 4273 (MO); Hidalgo: *King* 4231 (NY); Oaxaca: *Calderon* 1381 (MEXU); San Luis Potosi: *King* 4295 (NY); Tabasco: *Cowan & Zamudio* 3356 (MO); Veracruz: *Purpus* 7767 (NY). **Belize**, Cayo: *Gentle* 9020 (NY); Stann Creek: *Gentle* 8238 (F); Toledo: *Gentle* 5105 (F). **Guatemala**, Alta Verapaz: *Standley* 89745 (NY); Baja Verapaz: *Standley* 90970 (F); Chimaltenango: *Standley* 62133 (F); Escuintla: *Standley* 64566 (F); Izabal: *Steyermark* 41807 (F); Petén: *Steyermark* 45527 (F); Quezaltenango: *Steyermark* 33532 (F); Retalhuleu: *Standley* 88482 (F); San Marcos: *Standley* 68701 (F); Santa Rosa: *Standley* 78352 (F). **Honduras**, Atlantida: *Molina* 25654 (MO); Comayagua: *Standley* 13691 (MO); Cortez: *Molina* 6708 (NY); Olancho: *Standley* 18682 (F); Puerto Sierra: *Wilson* 395 (NY). **Nicaragua**, El Cabo: *Molina* 15068 (NY); Zelaya: *Stevens* 6826 (F). **Costa Rica**, Alajuela: *Lent* et al. 3384 (MO); Cartago: *Lent* 2355 (NY); Guanacaste: *Standley & Valerio* 45050 (ILL); Heredia: *Opler* 745 (MO); Puntarenas: *Haber* 1127 (MO, BM). **Panama**, Bocas del Toro: *Croat & Porter* 16244 (MO); Canal Zone: *Croat* 6319 (MO); Chiriquí: *Mori & Kallunki* 5918 (MO); Darien: *Gentry & Mori* 13893 (MO); Panama: *Croat* 14520 (MO). **Colombia**, Antioquia: *Haught* 4729 (ILL); Boyaca: *Lawrence* 681 (K); Caldas: *Pennell* 9075 (ILL); El Meta: *Philipson* et al. 2136 (BM); Valle: *Cuatrecasas* 21639 (ILL). **Venezuela**, Bolivar: *Steyermark* 88978 (K, NY); Caracas: *Buschel* s.n. (K); Falcón: *Steyermark* 99339 (K). **Surinam**, Lucie River: *Irwin* et al. 54650 (K, NY). **Bolivia**, without location: *Bang* 2640 (K). **Ecuador**, Los Rios: *Mexia* 6616 (ILL); Pichincha: *Holmgren* 835 (B). **Peru**, Hualgayoc: *Hutchison & Bismarck* 6386 (K); Huanuco: *Mexia* 8130 (K); Pachitea: *Schunke* 1619 (F, K). **Brazil**, Rio de Janeiro: *Glaziou* 4922 (K).

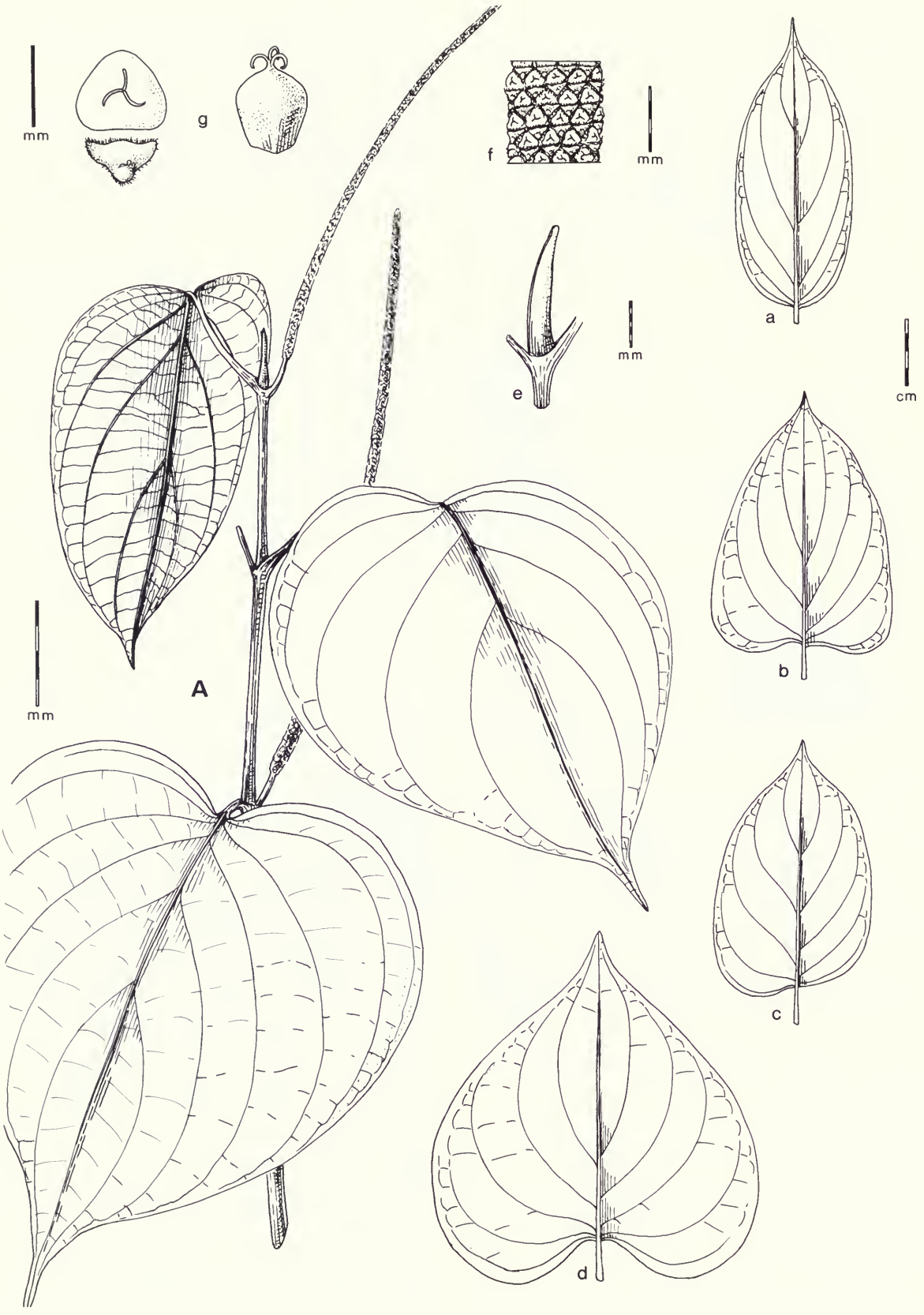

Fig. 24 *P. schiedeanum* A: habit; a–d: leaf variation; e: prophyll; f: part of inflorescence; g: bract and fruit.

Fig. 25 Distribution of *P. schiedeanum*.

This species has an extensive range that stretches from Mexico to Brazil, and is one of the most phenotypically plastic species in this section. It grows in shaded places of moist lowland forest, lower montane forest, wet ravines, and on the banks of streams and rivers. It displays great variation in leaf size and shape, ranging from elliptic-lanceolate or ovate to cordiform, frequently on the same plant; this plasticity can make correct identification difficult, something that is reflected in the large number of taxa that have been described in the past. Gomez Pompa (1966) has described the extreme vegetative variations to be found in this species. He reduced four species to synonymy (*P. megalophyllum* C. DC., *P. variabile* C. DC., *P. zacuapanum* C. DC., and *P. middlesexense* Trel.), and suggested that *P. carrilloanum* C. DC. and *P. casimirianum* Hemsley might also belong to *P. schiedeanum*.

For this study, large numbers of specimens of *P. carrilloanum* (including type material), and the type of *P. casimirianum*, were examined. It has proved impossible to separate these species satisfactorily from *P. schiedeanum* for, while there is a continuous variation in leaf shape and size, the inflorescence structure remains constant. The bracts partially cover the fruit in early stages of development, and the fruit is trigonous and glabrous. *Piper schiedeanum* has frequently been confused with *P. aequale*, and the inflorescence structures are very similar. *Piper aequale* can be distinguished by its dark, acute prophylls, bracts that do not appear to cover the fruits at any stage, and leaves that are acute to cuneate at the base. *Piper schiedeanum* has pale, blunt-tipped prophylls, bracts that cover the fruits at early stages, and leaves with ovate to deeply cordate bases. *Piper corrugatum* and *P. veraguense* are similar in inflorescence structure to *P. schiedeanum*, with floral bracts that often cover the fruits in early stages, but can be separated by their distinctive leaves.

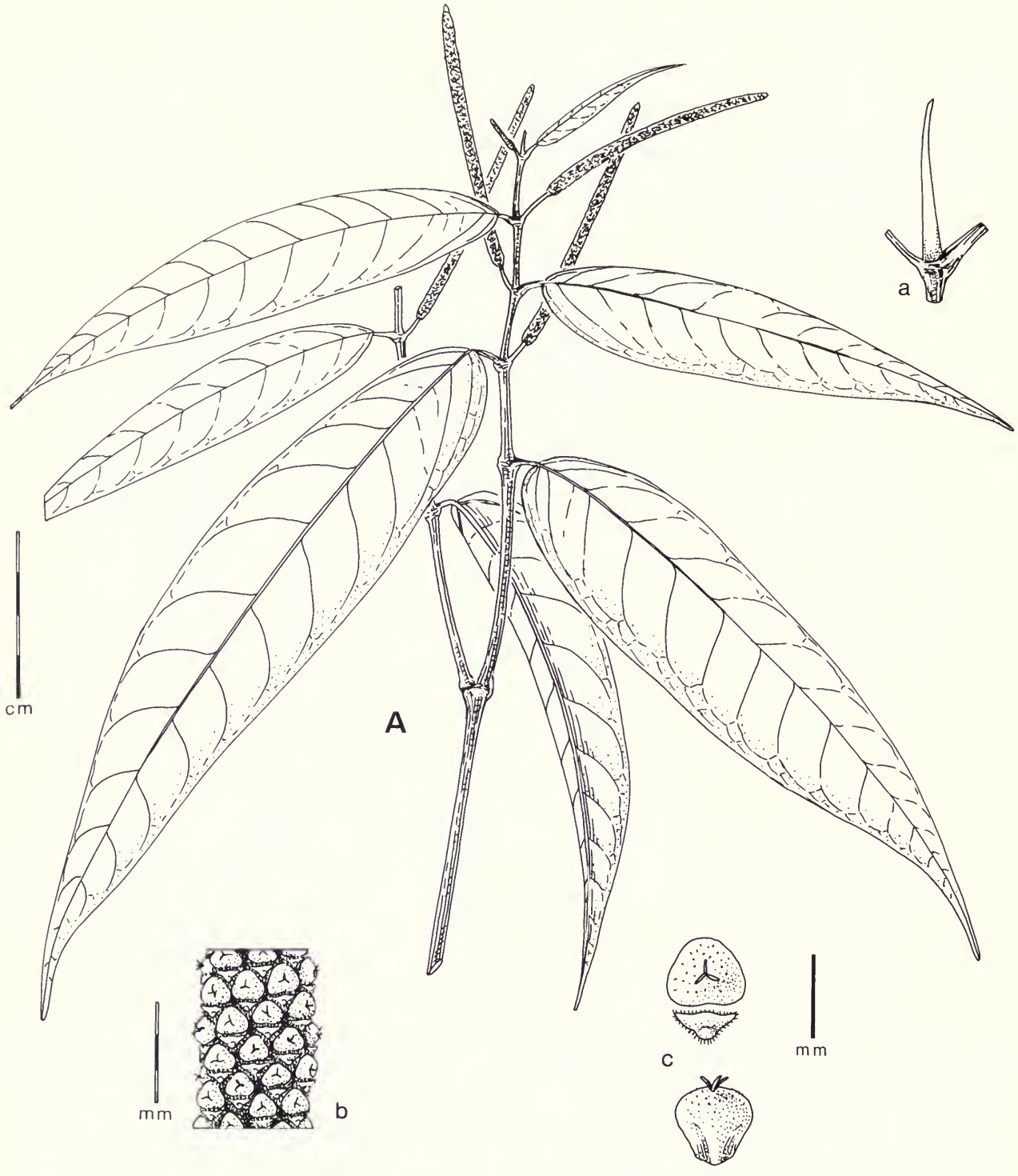

Fig. 26 *P. cadenaensis* A: habit; a: prophyll; b: part of inflorescence; c: bract and fruit.

39. **Piper cadenaensis** Tebbs, **sp. nov.** Type: Guatemala, Poptun Road, Cadenas, Petén, *Lundell & Contreras* 19010 (MO!-holotype).
Fig. 26.

Frutex 2–3 m altus. Folia anguste lanceolata glabra subcoriacea, apice acuminata basin rotundata interdum inaequalia. Spica erecta, bracteis ciliatis triangularibus. Bacca trigona apicem versus granulosa vel pilis minutis obtecta.

Shrub 2–3 m high, stems glabrous. Leaves 13–22 cm long, 3–6 (–7.5) cm wide, lanceolate, slightly curving, glabrous, subcoriaceous, pale green, apex narrowly acuminate, base rounded or slightly unequally lobed. Venation with 1–3 pairs

Fig. 27 Distribution of *P. cadenaensis*.

of secondary veins arising from the lower half of the prominent midrib and ascending to apex, and numerous cross-veins arising along the length of the midrib. Petioles 4–8 mm long, glabrous. Prophylls 4–12 mm long, narrow, glabrous, apex blunt. Inflorescences 3.5–7 cm long, erect; peduncles 4–8 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, triangular, fleshy, densely ciliate. Fruit obovoid, 0.7–1 mm wide, trigonous, minutely pubescent or granular; stigmas 3, linear.

Forest-covered hillsides; 0–200 m.

DISTRIBUTION. Guatemala. Fig. 27.

Guatemala, Izabal: *Contreras* 9051 (MO); Petén: *Lundell & Contreras* 19010 (MO).

This species superficially resembles *P. schiedeanum*, but can be distinguished by its distinctive lanceolate leaves with numerous cross-veins, shorter inflorescences, and pubescent or granular fruits. It is confined to the drier lowland areas of north-eastern Guatemala.

40. **Piper regnellii** (Miq.) C. DC. in DC., *Prodr.* **16**(1): 307 (1869).
Fig. 29A, a.

Artanthe regnellii Miq. in *Linnaea* **22**: 574 (1849). Type: Brazil, prov. Minas Gerais, Caldas, *Regnell* II 256 (S-holotype; C!, K!, US!-isotypes).
Piper epunctulatum C. DC. in DC., *Prodr.* **16**(1): 338 (1869). Type: Brazil, Minas Gerais, *Lindberg* 486 (M-holotype; S-isotype).
P. pallescens C. DC. in *Linnaea* **37**: 362 (1872). Type: Brazil, Lagoa Santa. *Warming* s.n. (C!-holotype).
P. fulvescens C. DC. in *Ann. N.Y. Acad. Sci.* **7**: 214 (1892). Type: Central Paraguay, *Morong* 760 (NY-holotype; K!-isotype).
P. fulvescens var. *subglabrum* C. DC. in *Mém. Soc. Phys. Hist. nat. Genève* **32**: 8 (1893). Type: Paraguay, Villa Rica, *Balansa* 2321 (G-holotype).
P. flabellinerve C. DC. in *Bot. Jb.* **65**: 26 (1901). Type: Brazil, Goiás, *Ule* 461 (P-isotype).
P. fulvescens var. *geraense* C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 436 (1917). Type: Brazil, Serra de Caldas, *Mosen* 1027 (S-holotype).
P. regnellii var. *glabrius* C. DC. in *Candollea* **1**: 273 (1923), nom. nud. (Art. 32.1).
P. regnellii var. *parvifolium* C. DC. in *Candollea* **1**: 273 (1923), nom. nud. (Art. 32.1).
P. regnellii var. *pallescens* (C. DC.) Yuncker in *Hoehnea* **2**: 172 (1972).

Shrub (1–) 2–4 m high, stems glabrous to shortly pubescent. Leaves 9–25 cm long, 8–22 cm wide, pale green, glabrous to minutely pubescent or velutinous, apex short-acuminate, base shallowly to deeply cordate. Venation with 3–6 pairs of secondary veins, mostly arising from the base, ascending at an acute angle to the apex. Petioles 4–9 cm long, vaginate to middle or above, sheathing the stems, glabrous to minutely pubescent. Prophylls 2–3 cm long. Inflorescences 6–15 cm long; peduncles 8–25 mm long. Anthers 0.5 mm long. Floral bracts 0.7–0.8 mm wide, orbicular-triangular, fleshy, white-ciliate. Fruit obovoid, 0.8–1 mm wide, glabrous; stigmas 3, linear.

Moist places in forest shade, steep wooded slopes, boggy ground, and stream sides; 400–1100 m.

DISTRIBUTION. Brazil to Argentina. Fig. 28.

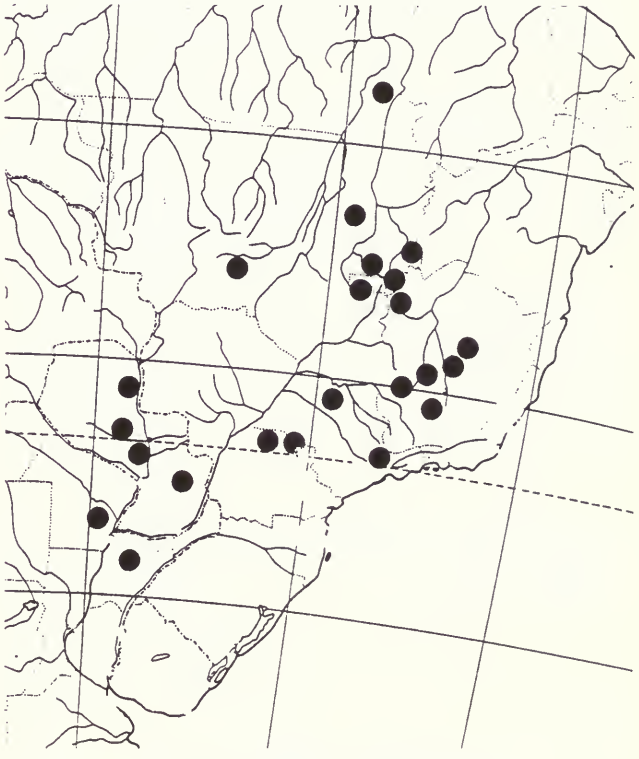

Fig. 28 Distribution of *P. regnellii*.

Brazil, Distrito Federal: *Prance & Silva* 59025 (K); Goiás: *Heringer* 8467 (NY); Matto Grosso: *Lankester* s.n. (K); Minas Gerais: *Bareto* 1816 (NY); Paraná: *Dusen* 9620 (K, NY); Rio de Janeiro: *Glaziou* 11577 (K); Santa Catarina: *Kummrow & Oliveira* 2318 (MU); São Paulo: *Hoehne & Gehrt* s.n. (NY). **Paraguay**, Central: *Pederson* 4238 (C); Cordillera: *Schwarz* 11083 (BM); Misiones: *Pedersen* 6551

Fig. 29 A: *P. regnellii*, habit; a: bract and fruit. B: *P. veraguense*, habit; b: part of inflorescence; c: bract and fruit.

(B,K); Paraguari: *Sparre & Vervoorst* 641 (K); San Pedro: *Woolston* 1336 (K); Sierra de Maracayu: *Hassler* 4788 (BM). **Argentina**, Itusaingo: *Meyer* 6263 (F); Santo Tomé: *Pedersen* 2909 (C).

Piper regnellii grows in moist, partially shaded places in gallery forest, mostly at about 1000 m altitude. It is one of the few species of *Piper* with a distribution stretching as far south as Argentina. The wide, usually shallowly cordiform leaves, together with the 2–3 cm long prophylls, and partly sheathing petioles, distinguish this species from other members of the section. There is considerable variation in the depth of the basal lobing of the leaves, often on the same individual.

41. **Piper veraguense** C. DC. in DC., *Prodr.* **16**: 294 (1869). Type: Costa Rica et Veragua, *Warscevicz* 1 (G-holotype; MO!-photograph).
Fig. 29B, b, c.

P. peltaphyllum C. DC. in *Bull. Soc. r. Bot. Belg.* **30** (1): 220 (1892). Type: Costa Rica, Route de Carillo, *Pittier* 2522 (G-holotype).
P. grandilimbum C. DC. in *Bot. Gaz.* **70**: 172 (1920). Type: Guatemala, *Türckheim* 8743 (US-holotype; F!-photograph).
P. albert-smithii Trel. & Yuncker, *Piperac. N. South. Amer.* **1**: 413 (1950). Type: Colombia, vicinity of El Roble, Dept. Santander, *Killip & Smith* 19360. (US-holotype; NY!-isotype).
P. mutisii Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 414 (1950). Type: Colombia, *Mutis* 3463 (MA-holotype; ILL!-photograph).
P. veraguense var. *mutisii* (Trel. & Yuncker) Steyerm. in *Fl. Venezuela* **2**: 590 (1984).
P. veraguense var. *venezuelense* Steyerm. in *Fl. Venezuela* **2**: 590 (1984). Type: Venezuela, Trujillo, *Breteler* 4082 (VEN-holotype).

Herb 1–2 m high, stems few, slender, erect, glabrous, sometimes rooting at nodes. Leaves 16–34 cm long, 10–22 (–28) cm wide, peltate or subpeltate, hanging vertically from petiole, ovate-lanceolate, coriaceous, glabrous or sparsely pubescent on the undersides, tapering to long-acuminate apex. Venation with 4–6 pairs of secondary veins arising from or near petiole attachment, radiating outwards and curving towards apex, and 2–3 pairs of secondary veins arising from further up the midrib, curving towards apex. Petioles 9–22 cm long. Prophylls 1.5–4 cm long, glabrous, apex blunt. Inflorescences 7–16 cm long, erect; peduncles 1–2 cm long. Anthers 0.2–0.3 mm long. Floral bracts 0.6–1 mm wide, triangular-rhomboid, minutely ciliate, concealing fruit in early stages. Fruit obovoid, trigonous, 1–1.2 mm wide, glabrous; stigmas 3.

Moist forest, shaded disturbed ground, and stream sides; 500–1900 m.

DISTRIBUTION. Mexico to Peru. Fig. 30.

Mexico, Chiapas: *Breedlove* 26096 (LAM, MO). **Guatemala**, Alta Verapaz: *Türckheim* II 1063 (MO); Huehuetenango: *Steyermark* 49216 (F); Petén: *Steyermark* 45372 (F). **Honduras**, Atlantida: *Standley* 53357 (F). **Nicaragua**, Jinotega: *Stevens* et al. 16531 (MO, BM). **Costa Rica**, Cartago: *Lent* 2745 (NY). **Panama**, Darien: *Folsom* 4299 (MO). **Venezuela**, Mérida: *Nees & Whalen* 16942 (VEN); Trujillo: *Liesner* et al. 12840 (MO, VEN). **Peru**, San Martin: *Schunke* 6258 (CAS).

Although the inflorescence of *Piper veraguense* is very similar to that of *P. schiedeanum* and *P. corrugatum*, the distinctive peltate leaves, hanging vertically from the petioles, make this species easily recognizable. *Piper scutilimbum* also has peltate leaves, but these are oblong-elliptic, with abruptly narrowed bases and long sheathing petioles; it also has much smaller (0.4 mm) floral bracts than *P. veraguense*.

Steyermark (1984) divided Venezuelan *P. veraguense* into three varieties. In his treatment, varieties *mutisii* and *venezuelense* were separated from the type variety by the differing degrees of pubescence on the veins of their leaves. This pubescence can be found to a greater or lesser extent in many specimens of *P. veraguense* outside Venezuela, and in this

Fig. 30 Distribution of *P. veraguense*.

Fig. 31 Distribution of *P. perbrevicaule*.

Fig. 32 A: *P. perbrevicaule*, habit; a: part of stem; b: part of inflorescence; c: bract and fruit. B: *P. reptabundum*, habit; d: part of inflorescence; e: bract and fruit; f: fruit.

treatment the variation is considered insufficiently distinct to maintain any division within the species.

42. **Piper perbrevicaule** Yuncker in *Ann. Mo. bot. Gdn* **37**: 51, fig. 9 (1950). Type: Panama, vicinity of Chiriquí Lagoon, Water Valley, Bocas del Toro, *von Wedel* 971 (MO!-holotype).
Fig. 32A, a, b, c.

P. perbrevicaule var. *subglabrilimbum* Yuncker in *Ann. Mo. bot. Gdn* **37**: 51 (1950). Type, Panama, Bocas del Toro, *von Wedel* 1074 (MO!-holotype).

Terrestrial or epiphytic herbs, stems 15–50 cm long, prostrate or trailing, often rooting at nodes, densely pubescent with long multicellular hairs. Leaves 6–12 cm long, 2.5–5 cm wide, asymmetrically oblong-elliptic to ovate-elliptic, often long-villous on both sides, sometimes bullate, apex acute-acuminate, base with one side lobed and overlapping petiole. Venation with 3–4 pairs of secondary veins loop-connecting to apex. Petioles 5–10 mm long, densely pubescent. Prophylls 8–12 mm long, sparsely to densely pubescent. Inflorescences 2–4 cm long, erect in early stages, greenish, white, pink or reddish-purple; peduncles (1–) 2–5 cm long, slender, curving. Anthers 0.3–0.4 mm long. Floral bracts 0.3–0.4 mm wide, triangular, glabrous to minutely pubescent. Fruit obovoid, 0.8–1 mm wide, trigonous, glabrous or granular, with domed apex; stigmas 3.

Moist places on floor of lower montane rain-forest, edges of forest trails, and banks of streams; 0–700 m.

DISTRIBUTION. Costa Rica, Panama. Fig. 31.

Costa Rica, Alajuela: *Grayum* et al. 6305 (BM, MO); Heredia: *Grayum* et al. 6155 (BM, MO). **Panama**, Bocas del Toro: *Wedel* 1469 (MO); San Blas: *Nevers* et al. 5048 (MO, BM); Veraguas: *Croat* 25648 (MO).

Piper perbrevicaule is a decumbent, succulent plant with stems barely reaching 50 cm in length, creeping along the banks of streams and growing on fallen logs, or occasionally found as an epiphyte. It is easily recognized by its densely pubescent stems, often bullate leaves, and inflorescences on long, slender peduncles. The scandent *P. reptabundum* also has long, slender peduncles and similarly shaped leaves, but does not share the copious pubescence and the sometimes bullate leaves of *P. perbrevicaule*. Long, slender peduncles are also found in *P. dolichotrichum*, a shrubby climber, and in *P. urostachyum* Hemsley of section *Callianira*.

A form of *P. perbrevicaule* from Costa Rica has peduncles of only 1 cm or less, rather than the 2–5 cm normally found. Although the specimens that have been seen are not fully mature, they are herbs of the forest understorey, and display the other characters found in this species, such as asymmetrical leaves, long, multicellular hairs, minute, triangular bracts, and glabrous or granular fruits.

43. **Piper reptabundum** C. DC. in *Bot. Gaz.* **70**: 169 (1920). Type: Costa Rica, Forêts de Shirores, Talamanca, Limón, *Tonduz* 9277 (G-holotype; F!, US!-isotypes).
Fig. 32B, d, e, f.

Scandent, with glabrous stems. Leaves 10–18 cm long, 3–6 cm wide, narrowly asymmetrically oblong-elliptic to oblong-lanceolate, rough above, glabrous below, apex narrowly long-acuminate, base sometimes slightly lobed on one side.

Fig. 33 Distribution of *P. reptabundum*.

Venation with 3–5 pairs of secondary veins arising from the length of the midrib, loop-connecting to apex. Petioles 1–5 mm long, glabrous. Prophylls 5–10 mm long, slender. Inflorescences 5–10 cm long, greenish pink, curving and becoming pendulous in fruit, on slender, glabrous peduncles 4–6 (–7) cm long. Anthers 0.3–0.5 mm long. Floral bracts 0.5–0.8 mm wide, broadly triangular, fleshy, glabrous or minutely ciliate. Fruit obovoid, 0.8–1 mm wide, trigonous, minutely granular above, with domed apex; stigmas 3, recurved.

Growing in moist places in forest shade, often near streams; 0–600 m.

DISTRIBUTION. Costa Rica. Fig. 33.

Costa Rica, Limón: *Burger* et al. 10400 (F, MO); San José: *Croat* 35274 (MO).

Piper reptabundum is closely related to *P. perbrevicaule*, with asymmetric leaves, curved or arching inflorescences on long slender peduncles, and fruits with minutely granular surfaces. It can be distinguished by its much longer, narrow leaves with scarcely any basal lobing, absence of multicellular hairs, and more robust habit. *Piper dolichotrichum* also has long, slender peduncles, but can be distinguished from *P. reptabundum* by its vigorous climbing habit up to 7 m high, elliptic-ovate leaves, long multicellular hairs, and bracts thickly fringed with hairs. Unfortunately *P. reptabundum* has not been widely collected, and only a few specimens from scattered locations in Costa Rica have been seen. Although there is some variation in leaf width between these populations, they all share the distinctive leaf asymmetry, narrow, sharply pointed apices, and inflorescences with long filiform peduncles.

44. **Piper fortunaensis** Tebbs, **sp. nov.** Type: Panama, vicinity of Fortuna Dam, Chiriquí, *McPherson* 9832 (MO!-holotype).
Fig. 34.

Frutex 1–1.5 m altus. Folia elliptica asymmetrica glabra glandulosa apice acuminata basin acuta vel cuneiformia. Spica erecta, bracteis gibbosis triangularibus. Bacca trigona apicem versus granulosa.

Spindly shrub 1–1.5 m high, stems glabrous. Leaves 14–21 cm long, 3–8.5 cm wide, asymmetrically narrowly to broadly

Fig. 34 *P. fortunaensis* A: habit; a: prophyll; b: part of inflorescence; c: bract and fruit.

elliptic, glabrous, glandular, apex long-acuminate, base acute to cuneate. Venation with 2–4 pairs of secondary veins arising from the lower half of the midrib, and 1–2 pairs from the upper half, curving to apex. Petioles 4–8 mm long, glabrous. Prophylls 1–4 cm long, narrow, apex acute. Inflorescences 4–8 cm long, erect, green or white; peduncles 5–10 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.7–0.8 mm wide, fleshy, oblong-triangular, gibbous, glabrous. Fruit obovoid, 1 mm wide, trigonous, upper surface granular, glandular; stigmas 3.

Damp places in high forest; 600–1500 m.

DISTRIBUTION. Costa Rica, Panama. Fig. 35.

Costa Rica, Heredia: *Grayum* et al. 5067 (MO). **Panama**, Bocas del Toro: *Gordon* 53D; *McPherson* 9667 (MO); Chiriquí: *D'Arcy* 16358B; (MO); Veraguas: *Antonio* 3536 (MO).

Piper fortunaensis has similarly shaped leaves, bracts, and fruits to *P. reptabundum*. It can be identified by its shrubby habit, long narrow prophylls, and short peduncles. Its distinctive, fleshy, glabrous bracts also serve to distinguish it from those of *P. aequale*, which are ciliate. Most of the specimens examined were collected from the Fortuna Dam area, which has produced a number of interesting plants. It has been recorded on one collection (*Gordon* 53D) that this plant is a 'fish-poisoning shrub.'

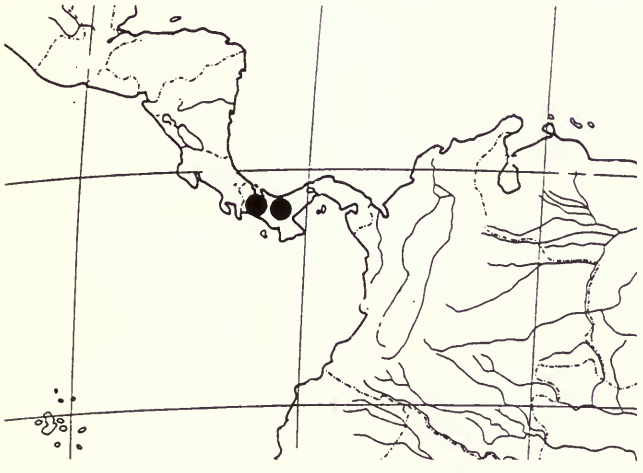

Fig. 35 Distribution of *P. fortunaensis*.

45. **Piper dolichotrichum** Yuncker in *Amer. J. Bot.* **39**: 635 (1952). Type: Colombia. Nariño, Gorgona Island, *Collenette* 524 (K!-holotype; US!-isotype).
Fig. 37A, a.

Shrubby liana 1–5 (–7) m high, occasionally epiphytic, stems usually covered with multicellular hairs 1–3 mm long. Leaves 12–24 cm long, 6–12 cm wide, narrowly to widely elliptic-ovate, upper surface with scattered hairs, undersurface sparsely to densely pubescent, glandular, apex long-acuminate, base unequally shallowly lobed. Venation with 5–7 pairs of prominent secondary veins ascending sharply to apex. Petioles 3–12 mm long, densely long-pubescent. Prophylls 7 mm long, narrow, with long multicellular hairs. Inflorescences 3.5–7 cm long, pendulous, sometimes with a short sterile tip, greenish white; peduncles 2–3 cm long, slender, densely covered in multicellular hairs. Anthers 0.1–0.3 mm long. Floral bracts

Fig. 36 Distribution of *P. dolichotrichum*.

0.8 mm wide, lunulate to widely triangular, ciliate. Fruit obovoid, 1–1.2 mm wide, trigonous, often glandular; stigmas 3, sessile.

In marshy or damp areas of moist forest; 0–800 m.

DISTRIBUTION. Costa Rica–Ecuador. Fig. 36.

Costa Rica, Heredia: *Burger* 8074 (F); Limón: *Solis* 23435 (BM); Puntarenas: *Burger & Liesner* 7310 (F). **Panama**, Chiriquí: *Him & Gordon* 500 (MO); Veraguas: *Maas & Dressler* 1643 (F). **Colombia**, Choco: *Hugh-Jones* 306 (K). **Ecuador**, Esmeraldas: *Mexia* 8411 (BM).

Piper dolichotrichum is one of several climbing species in *Piper*, and is capable of reaching 7 m in height. It is similar to the shrubby *P. urostachyum* of section *Callianira*, which also has long multicellular hairs, pendulous inflorescences on slender peduncles, and long prophylls. However, the fruits of *P. dolichotrichum* are obovoid, trigonous and lack a style, whereas those of *P. urostachyum* are globose or hemispherical, and have a distinct elongated style. Sterile specimens of *P. dolichotrichum* appear similar to the scandent *P. brachypodon*, which also has ovate-elliptic leaves with prominent veins. However, *P. brachypodon* has glabrous, often maculate stems, and the leaves are larger and thicker than those of *P. dolichotrichum*.

46. **Piper subsessilifolium** C. DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 216 (1892). Type: Costa Rica, Rio Navarrito, *Pittier* 2435 (G-holotype, photograph!).
Fig. 39A, a, b, c.

P. flavirameum C. DC. in *Bot. Gaz.* **70**: 181. (1920). Type: Costa Rica, forêts de la Palma, *Pittier* 12510 (G!-holotype).
P. arundinetorum Trel. in *Contr. U.S. natn. Herb.* **26**: 159 (1929). Type: Costa Rica, near Laguna de la Escuadra, San José, *Standley* 41967 (US-holotype).
P. concepcionis Trel. in *Contr. U.S. natn. Herb.* **26**: 159 (1929). Type: Costa Rica, La Concepción, *Donnell Smith* 6749 (US!-holotype).

Fig. 37 A: *P. dolichotrichum*, habit; a: bract and fruit. B: *P. brachypodon*, habit; b: bract and fruit.

P. pendens Trel. in *Contr. U.S. natn. Herb.* **26**: 160 (1929). Type: Costa Rica, Yerba Buena, San Isidro, Heredia, *Standley & Valerio* 49822 (US-holotype, photograph!).

P. pendens var. *infaustum* Trel. in *Contr. U.S. natn. Herb.* **26**: 160 (1929). Type: Costa Rica, El Muñeco, S. of Navarro, Cartago, *Standley 33651* (US-holotype, photograph!).

P. sulcinervosum Trel. in *Contr. U.S. natn. Herb.* **26**: 159 (1929). Type: Costa Rica, Cerro de la Carpintera, Cartago, *Standley* 35569 (US-holotype).

P. flavirameum var. *obscurum* Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 343 (1937). Type: Costa Rica, *Brenes* 20629 (F!-holotype).

P. debilicaule Trel. & Yuncker, *Piperac. N. South. Amer.* **1**: 333 (1950). Type: Ecuador, Parroquia Concepción, Playa Rica, Esmeraldas, *Mexia* 8411 (US-holotype; BM!, K!-isotypes).

Climbing or scrambling liana, 2–4 (–5) m high, stems glabrous to minutely puberulent, zig-zagging. Leaves 13–28 cm long, 6–17 cm wide, dark green and lustrous above, membranous, paler on underside, narrowly to widely elliptic-ovate, glabrous to minutely puberulent, apex acute-acuminate, base narrowing to small, rounded, unequal lobes. Venation with 3–5 pairs of secondary veins arising from lower half of midrib, ascending sharply to apex, prominent beneath. Petioles 3–10 mm long, pubescent. Prophylls 1–4 cm long, minutely pubescent, sometimes glandular. Inflorescences 3.5–8 (–10) cm long, erect, pink to purple, sometimes pendulous in fruit; peduncles 5–12 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.6–1 mm wide, triangular-lunulate, pink- to purple-ciliate. Fruit obovoid, 0.8–1.5 mm wide, trigonous, with minute style; stigmas 3.

Tropical wet forest, cloud and elfin forest, and damp shady spots in land cleared for agriculture or by logging; 0–2200 m.

DISTRIBUTION. Costa Rica to Ecuador. Fig. 38.

Costa Rica, Alajuela: *Lent* 2815 (F); Cartago: *Gomez* 18872 (CR); Heredia: *Garwood* et al. 939 (BM); Limón: *Davidson & Donahue* 8827 (NY); Puntarenas: *Haber* 5726 (MO); San José: *Lent* 3233 (F). **Panama**, Bocas del Toro: *Croat* 60165 (MO); Chiriquí: *Hampshire & Whitefoord* 18 (BM); Colón: *Dressler* 4656 (MO); Darien: *Kirkbride & Duke* 1160 (MO); Panama: *Croat* 22748 (F); Veraguas: *Mori & Kallunki* 2593 (MO). **Colombia**, El Valle: *Killip* 11814 (NY). **Venezuela**, Yaracuy: *Davidse* et al. 20689 (MO). **Ecuador**, Esmeraldas: *Asplund* 16304 (K); Imabura: *Acosta Solis* 12213 (F).

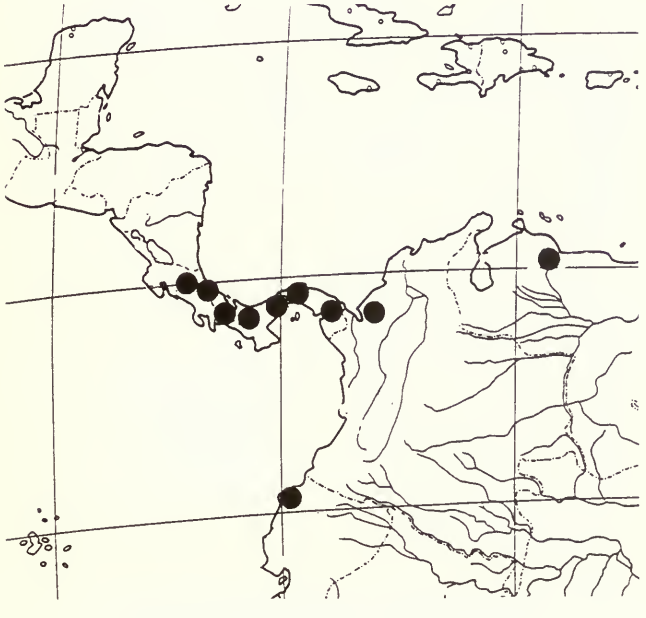

Fig. 38 Distribution of *P. subsessilifolium*.

A vigorous liana climbing trees, shrubs, and tree-ferns, with lateral branches often hanging downwards. The new leaves and flowering spikes are often wine-red or maroon to violet, and blend into the deep shade of the forest. The stem has a spicy or pungent aroma when crushed. It is related to *P. xanthostachyum*, but differs from this species by having a pink or purple, sometimes pendulous inflorescence, as opposed to a yellow-white and erect one, and larger, less angular floral bracts fringed with pink to purple hairs. *Piper concepcionis* has been reduced to synonymy here, as it is considered to be merely a broad-leaved form of *P. subsessilifolium*. It has the same type of leaf venation, and identical inflorescence characters, notably purple or pink colouring, bracts fringed with pink hairs, and trigonous fruits.

47. **Piper brachypodon** (Benth.) C. DC. in DC., *Prodr.* **16**(1): 327 (1869).
Fig. 37B, b.

Artanthe brachypoda Benth., *Bot. voy. Sulphur*: 167, pl. 54 (1844). Type: Colombia, Gorgona Island, *Hinds* s.n. (K!-holotype).

Straggling shrub, 1–5 m high, stems glabrous, red-streaked. Leaves (13–) 17–29 (–32) cm long, 8–16 (–20) cm wide, widely ovate-elliptic, glabrous, subcoriaceous, apex acute-acuminate, base slightly unequal. Venation with 4–7 pairs of secondary veins arising from lower to middle part of midrib, curving towards apex, prominent on underside. Petioles 7–15 mm long, glabrous. Prophylls 1–2 cm long, 8–12 mm wide. Inflorescences 3–5 (–7) cm long, erect; peduncles 2–5 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.8–1 mm wide, widely triangular, sometimes with pellucid glands, minutely ciliate. Fruit obovoid, 1 mm wide, apex domed, glabrous, with prominent glands; stigmas 3, recurved.

Dense moist forest; 0–300 m.

DISTRIBUTION. Colombia. Fig. 40.

Colombia, Barbacoas: *Triana* 17; Gorgona Island: *Collenette* 714 (K).

Piper brachypodon is a glabrous plant, with maculate stems, sub-coriaceous leaves with prominent veins, and glandular fruits. It can be compared with both *P. subsessilifolium* and *P. dolichotrichum* in leaf shape and venation, although it is a straggling shrub, rather than a climber. *Piper dolichotrichum* is copiously pubescent and has a slender inflorescence on a long, thin peduncle, making it easily separable from *P. brachypodon* when spikes are present. *P. subsessilifolium* can be distinguished by its deep red to purple, often pendulous inflorescences, while those of *P. brachypodon* are white or green, and erect. Both species have broadly triangular bracts, fringed with hairs.

48. **Piper xanthostachyum** C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 169 (1897). Type: Costa Rica, Bois de la vallée du Rio Tuis, *Pittier* 8158 (G-holotype; F!-photograph).

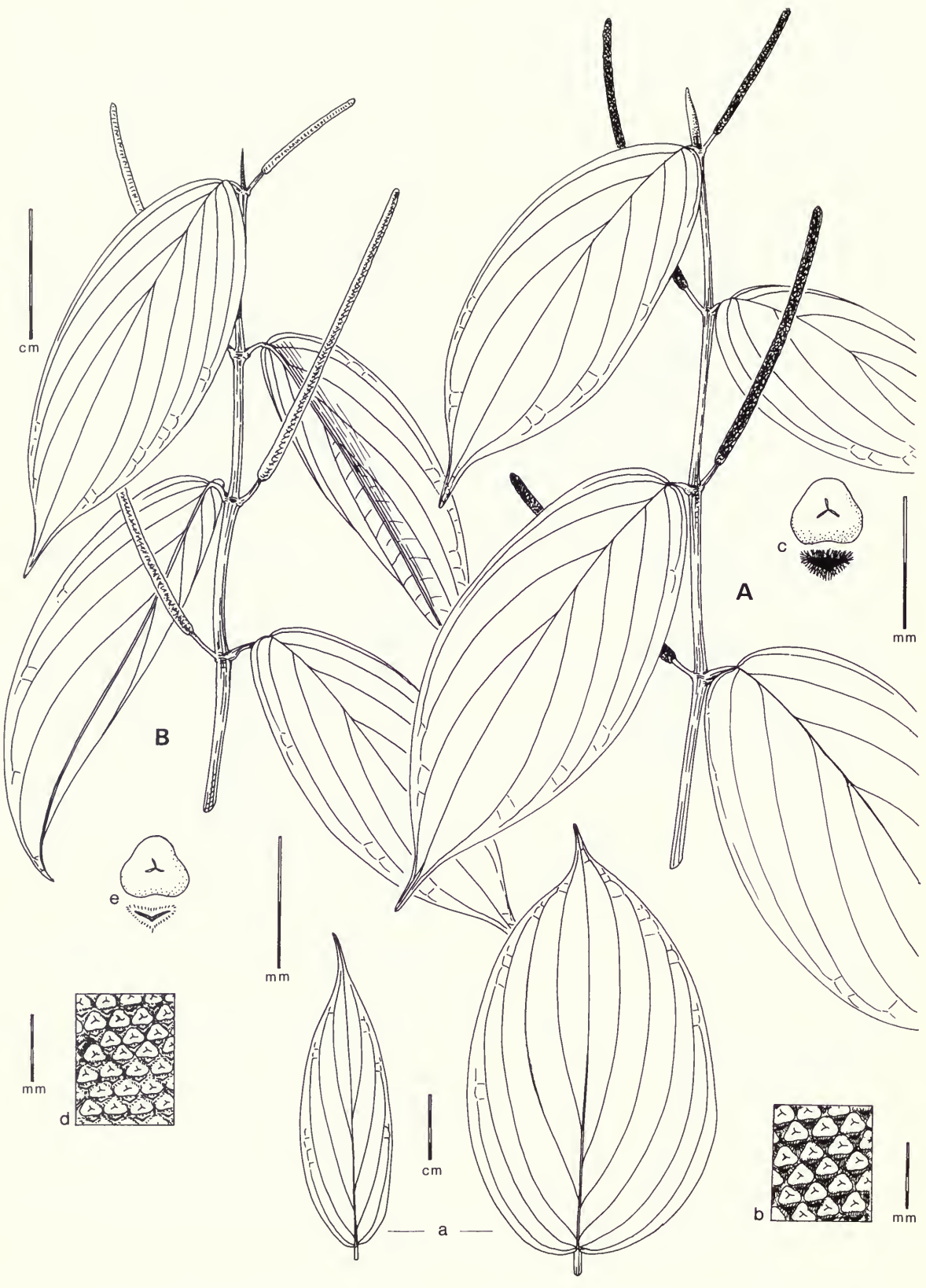

Fig. 39 A: *P. subsessilifolium*, habit; a: variation in leaf shape; b: part of inflorescence; c: bract and fruit. B: *P. xanthostachyum*, habit; d: part of inflorescence; e: bract and fruit.

Fig. 40 Distribution of *P. brachypodon*.

Fig. 39B, d, e.

P. matinanum C. DC. in *An. Inst. fís.-geogr. C. Rica.* **9**: 170 (1897). Type: Costa Rica, *Pittier* 9759 (G-holotype; US-isotype; MO!-photograph).

P. bryogetum C. DC. in *Bot. Gaz.* **70**: 175 (1920). Type: Costa Rica, *Tonduz* 12939 (G-holotype; MO!-photograph).

P. opacibracteum Trel. in *Contr. U.S. natn. Herb.* **26**: 148 (1929). Type: Costa Rica, N. of Tilarán, *Standley & Valerio* 45899 (US-holotype, photograph!).

Climbing or scrambling over low shrubs, or epiphytic, 1–2 m high, stems glabrous or minutely pubescent. Leaves 10–18 cm long, 3–8 cm wide, oblong to elliptic-lanceolate, glabrous on both surfaces, apex acute-acuminate, base narrowly obtuse. Venation with 3–4 pairs of secondary veins arising mainly from the lower half of midrib, arcuate-ascending. Petioles 4–10 mm long, glabrous. Prophylls 8–12 mm long, glabrous. Inflorescences erect, yellow-white, 5–12 cm long; peduncles 5–12 mm long, glabrous. Anthers 0.2–0.3 mm long. Floral bracts 0.3–0.5 mm wide, narrowly triangular to crescent-shaped, densely yellow-white-ciliate. Fruit obovoid, 0.8–1 mm wide, trigonous, with pellucid glands; stigmas 3, linear.

Pre-montane rain-forest, wet evergreen forest, or moist secondary forest; 0–2400 m.

DISTRIBUTION. Guatemala–Peru. Fig. 41.

Guatemala, Alta Verapaz: *Standley* 91383 (F); San Marcos: *Standley* 68570 (F). **El Salvador**, Santa Ana: *Molina* 12525 (F). **Honduras**, Intibuca: *Molina* 13990 (F); Francisco Morazán: *Morton* 7287 (F). **Costa Rica**, Alajuela: *Lent* 2653; Cartago: *Liesner* 14429 (MO); Puntarenas: *Liesner* 2018 (MO); San José: *Molina* et al. 18074 (MO). **Panama**, Darien: *Kirkbride & Duke* 1197 (MO). **Ecuador**, Pichincha: *Cazalet & Pennington* 5086 (K). **Peru**, San Martin: *Knapp & Mallet* 8385 (K, MO).

The leaves of this species are similar in shape and venation to those of *Piper subsessilifolium*, *P. dolichotrichum*, and *P. brachypodon*, and it can be difficult to distinguish sterile specimens of these taxa. However, the inflorescence characters of narrowly triangular to crescent-shaped bracts fringed with yellow to white hairs, and glandular fruits, easily separate *P. xanthostachyum* from these species. Comments on collectors' labels say that the leaves have a very spicy odour like *Lindera benzoin* Meissner (Spice Bush) when first crushed, or a lemon or lime fragrance. Burger (1971) united *P. matinanum* and *P. xanthostachyum* under the latter name and this choice should be followed (Art. 57.2).

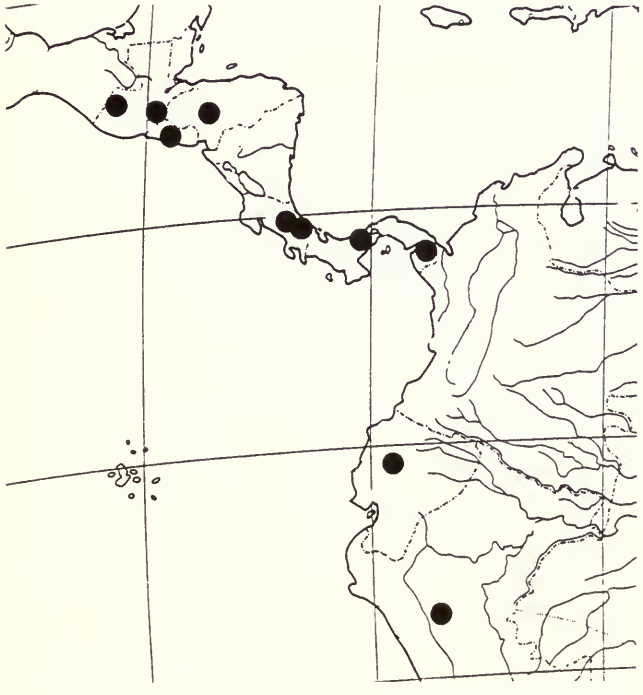

Fig. 41 Distribution of *P. xanthostachyum*.

49. **Piper ottoniifolium** C. DC. in *J. Bot., Lond.* **4**: 213 (1866) Type: Colombia, prov. del Choco, *Triana* 32 (G-holotype; BM!-isotype).

Fig. 43A, a.

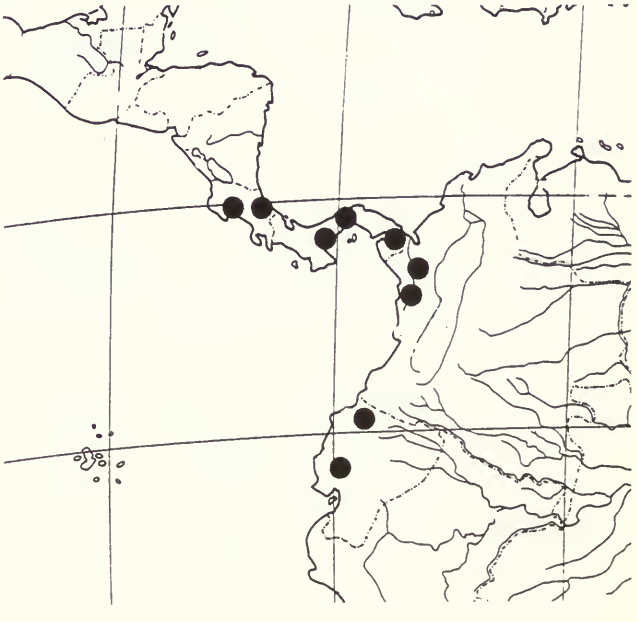

Fig. 42 Distribution of *P. ottoniifolium*.

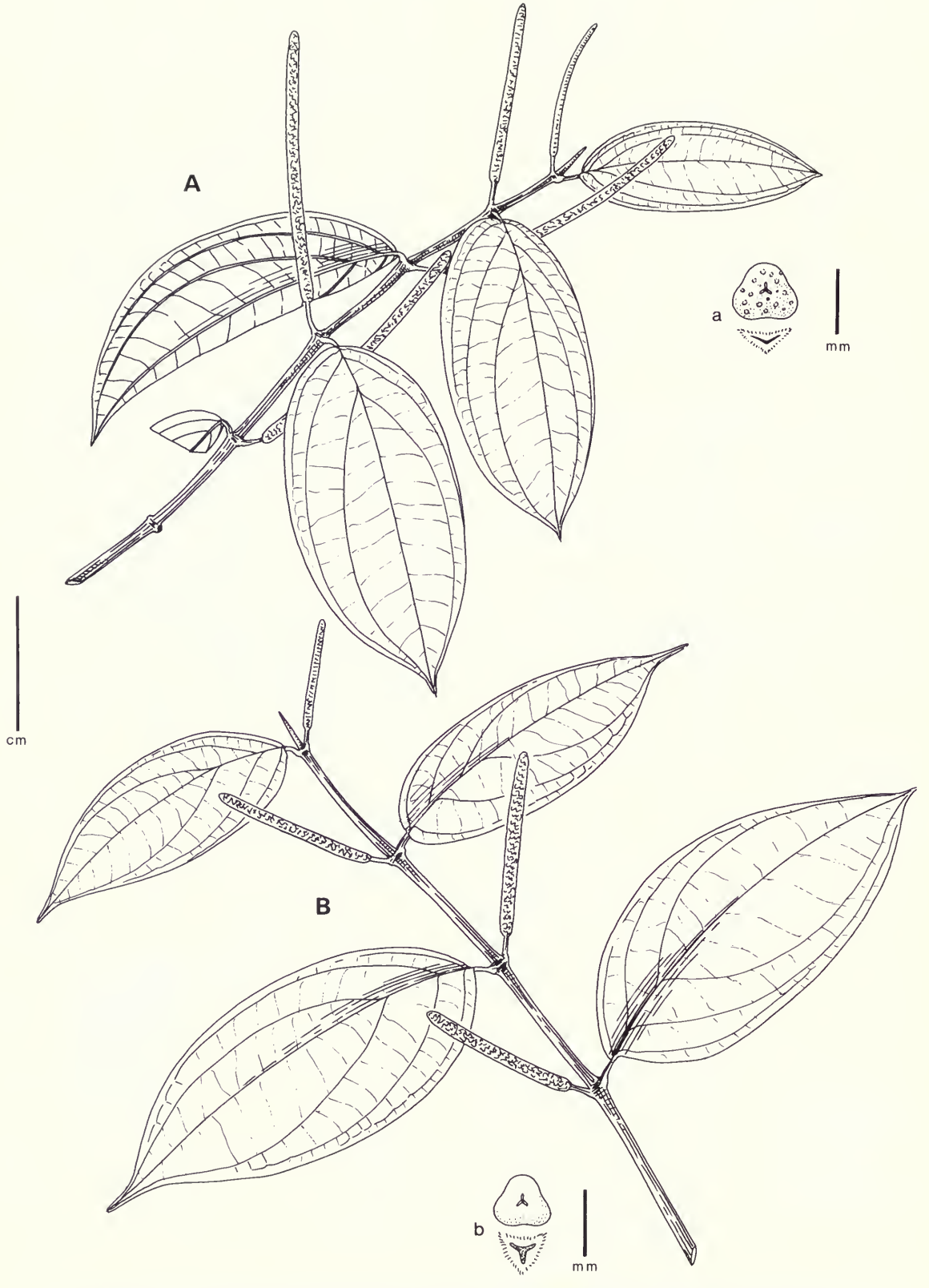

Fig. 43 A: *P. ottoniifolium*, habit; a: bract and fruit. B: *P. septuplinervium*, habit; b: bract and fruit.

P. scleromyelum C. DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 167 (1897). Type: Costa Rica, Bois de Tsuritkub, Talamanca, 100 m, *Tonduz* 8675 (G-holotype; F!, MO!-photographs).
P. ledezmae Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 82 (1950). Type: Colombia, near Quibdó, Chocó, *Killip & Ledezma* 35314 (US-holotype, photograph!).
P. ottoniifolium var. *frutescens* Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 87 (1950). Type: Colombia, *Killip & Cuatrecasas* 39164 (US-holotype; F!-isotype).
P. ottoniifolium var. *latifolium* Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 87 (1950). Type: Ecuador, Balao, *Eggers* 14434 (US-holotype).

Shrubby, scandent or epiphytic, stems glabrous or minutely puberulent, aromatic. Leaves 9–21 cm long, (3–) 5–9 (–11) cm wide, narrowly to broadly oblong-elliptic, coriaceous or subcoriaceous, glossy above, pale green or brown beneath, glabrous, glandular, apex acute-acuminate, occasionally mucronate, base unequally obtuse to cuneate, sometimes with very small lobes overlapping petiole. Venation with 2–3 (–4) pairs of prominent secondary veins arising from base, the upper pair curving to apex, crossed with reticulate veins. Petioles 2–10 mm long, glabrous. Prophylls 8–20 mm long, glabrous. Inflorescences 5–11 cm long, erect, pale green, often becoming pendulous in fruit; peduncles 6–10 mm long, glabrous. Anthers 0.2–0.5 mm long. Floral bracts 0.5–0.8 mm wide, sharply triangular to crescent-shaped, glandular, densely yellowish-white-ciliate. Fruit obovoid, 1 mm wide, trigonous, with prominent glands, apex conical; stigmas 3, linear.

Moist forest, and thickets by roads or tracks; 0–1300 m.

DISTRIBUTION. Costa Rica to Ecuador. Fig. 42.

Costa Rica. Limón: *Gomez* et al. 20390 (BM); Puntarenas: *Grayum & Hammel* 5637 (BM, MO). **Panama**, Colon: *Dressler* 3862 (MO); Darien: *Mori & Kallunki* 5468 (MO); Panama: *Busey* 908 (NY); Veraguas: *Gentry* 6219 (F). **Colombia**, Antioquia: *Araque & Barkley* 18c751 (BM); Cauca: *Cuatrecasas* 14168 (F); Choco: *Triana* 32 (BM); Valle: *Cuatrecasas* 15728 (F). **Ecuador**, near village of Bucay: *Camp* 3767 (BM); Carchi: *Madison* et al. 4578 (F).

The distinctive pale, coriaceous leaves with camptodromous venation and the usually climbing or scandent habit readily distinguish *P. ottoniifolium* from other species of *Piper*. It is most similar to the shrubby *P. septuplinervium*, which also has glossy, coriaceous leaves with similar venation. However, *P. septuplinervium* can easily be identified by its inflorescence characters of distinctive T-shaped bracts fringed with white hairs, and eglandular fruits. Burger (1971) suggested that *P. scleromyelum* might be synonymous with *P. ottoniifolium*, differing only in having much broader and thicker leaves. Only two specimens have been seen labelled as *P. scleromyelum*, both from Puntarenas in Costa Rica and both described as shrubs or small trees 2–3 m high. In characters such as leaf shape and venation, inflorescence, shape of floral bracts and glandularity of fruits, these specimens are certainly identical with *P. ottoniifolium*. As the original description and the photograph of the type compare favourably with those of *P. ottoniifolium*, *P. scleromyelum* has been placed here into synonymy.

50. **Piper septuplinervium** (Miq.) C. DC. in DC., *Prodr.* **16**(1): 313 (1869).
Fig. 43B, b.

Artanthe septuplinervia Miq. in Seemann, *Bot. voy. Herald*: 199, pl. 40 (1854). Type: Panama, without locality, *Seemann* 1066 (K-holotype; BM!-isotype).
Piper novo-granatense C. DC. in DC., *Prodr.* **16**(1): 313 (1869). Type: Colombia, Barbacoas, *Triana* 30 (G-holotype; BM!-isotype).
P. septuplinervium var. *subpubinervium* Yuncker in *Ann. Mo. bot. Gdn* **37**: 46 (1950). Type: Panama, *Sutton Hayes* 783 (NY!-holotype).

Slender shrub or small tree, 1–3 m high, stems glandular, glabrous or occasionally minutely pubescent on younger growth. Leaves 10–16 cm long, 5–8 cm wide, glabrous, glandular, lustrous above, paler beneath, coriaceous or subcoriaceous, elliptic-lanceolate, apex acuminate, base slightly unequally rounded. Venation with 3–5 pairs of secondary veins arising from lower to middle part of midrib, curving towards apex, with prominent cross-veins. Petioles 3–8 mm long, glabrous. Prophylls 10–15 mm long. Inflorescences 3–6 (–8) cm long; peduncles 4–10 mm long. Anthers 0.2 mm long. Floral bracts 0.6–0.8 mm wide, narrowly T-shaped, densely white-ciliate. Fruit obovoid, 0.8–1 mm wide, trigonous, glabrous; stigmas 3, sessile.

Mangrove swamps, clearings along river banks, and forest near coast; 0–400 m.

DISTRIBUTION. Panama–Ecuador. Fig. 44.

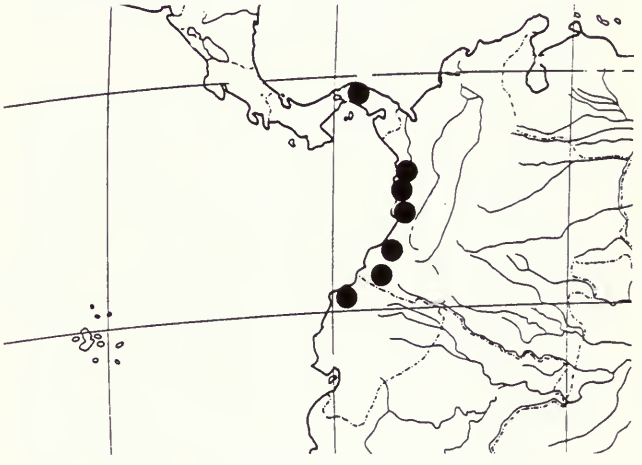

Fig. 44 Distribution of *P. septuplinervium*.

Panama, Colón: *Pittier* 2477 (G). **Colombia**, Altaquier, Cordillera Central: *Andre* 3355 (K); Choco: *Killip & Cuatrecasas* 39156 (US, BM); El Valle: *Killip* 34965 (BM). **Ecuador**, Esmeraldas: *Jativa & Epling* 2212 (S).

Piper septuplinervium can be distinguished by its shrubby habit, short inflorescence, and distinctive T-shaped bracts with a dense fringe of white hairs. It has similar leaves to the climbing *P. ottoniifolium*, with prominent secondary and cross-venation and lustrous upper surfaces, but the inflorescences of *P. ottoniifolium* are longer, and the bracts are crescent-shaped and fringed with yellowish white hairs. There can also be some confusion with the leaves of the shrubby *P. carpunya*, which are also glossy and coriaceous, but the bracts of this species are fleshy, cupulate, and glabrous.

51. **Piper coruscans** Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 53 (1816). Type: Crescit in ripa fluminis Magdalenae, inter S. Bartholeme et Garapatas, *Humboldt* 1629 (B-?holotype; F!-photograph).
Fig. 46A, a.

Schilleria coruscans (Kunth) Kunth in *Linnaea* **13**: 708 (1839).
Steffensia pseudochurumayu Kunth in *Linnaea* **13**: 662 (1839). Type: In Brazilia ad flumen Amazonum, *Poeppig* 3059 (B-holotype; G!-isotype).
Artanthe coruscans (Kunth) Miq., *Syst. piperac.*: 411 (1844).
A. pseudochurumayu (Kunth) Miq., *Syst. piperac.*: 407 (1844).
A. amazonica Miq. in *Linnaea* **20**: 146 (1847). Type: Brazil, Costa de Mattari, prov. Rio Negro, *Martius* s.n. (M-holotype, ILL!-photograph).
Piper amazonicum (Miq.) C. DC. in DC., *Prodr.* **16**(1): 272 (1869).
P. baryanum C. DC. in DC., *Prodr.* **16**(1): 272 (1869). Type: Brazil, *Riedel* 49 (L-holotype; K!-isotype).
P. pseudochurumayu (Kunth) C. DC. in DC., *Prodr.* **16**(1): 288 (1869).
P. pseudochurumayu var. *membranaceum* C. DC. in DC., *Prodr.* **16**(1): 288 (1869). Type: Ad flumina Casiquari, Vasiva et Pamoni, *Spruce* 3433 (G!-holotype; K!-isotype).
P. orenocanum C. DC. in *Bull. Herb. Boissier* **6**: 564 (1898). Type: Venezuela, ad flumen Orenoco, *Rusby & Squires* 267 (NY-holotype; ILL!-photograph).
P. wurdackii Yuncker in *Mem. N.Y. bot. Gdn* **10**(5): 41 (1964). Type: Venezuela, Cerro de la Neblina, *Maguire* et al. 42007 (NY-holotype; VEN-isotype).
P. coruscans var. *membranaceum* (C. DC.) Steyerm., *Fl. Venezuela* **2**: 383 (1984).

Shrub 1–4 m high, stems glabrous to minutely puberulent. Leaves 10–24 (–30) cm long, 6–19 cm wide, ovate to ovate-suborbiculate, membranous, lustrous and glabrous above with pellucid glands often present, minutely puberulent on veins below, sometimes rugose, apex acute-acuminate, base round to subcordate. Venation with 5–8 pairs of secondary veins mostly arising from the lower half of the midrib, ascending steeply to apex, prominent on underside. Petioles 0.5–6 cm long, glabrous to minutely puberulent. Prophylls 2–3 cm long, glabrous. Inflorescences 7–15 cm long, erect, pale green, yellow or white; peduncles 1–3 cm long. Anthers 0.3 mm long. Floral bracts 0.5 mm wide, triangular-orbicular, densely ciliate. Fruits obovoid, 0.8–1 mm wide, suborbicular-trigonous, with slight depression in centre, glabrous; stigmas 3.

Moist places in tropical evergreen forest, cliff bases and wet steep slopes, stream and river banks; 0–1700 m.

DISTRIBUTION. Colombia to Brazil. Fig. 45.

Colombia, Choco: *Molina & Barkley* 19Ch048 (K); Popayan: *Hartweg* 1398 (BM); Putumayo: *Klug* 1832 (BM); Santander: *Haught* 1699 (BM); Valle: *Cuatrecasas* 16658 (F). **Venezuela**, Amazonas: *Nee* 30828 (F); Apire: *Davidse & González* 14070 (MO); Bolivar: *Morillo & Liesner* 8960 (MO); Casiquari: *Spruce* 3433. **Ecuador**, Guayas: *Camp* 3586 (NY). **Peru**, Loreto: *Jones & Davidson* 9534 (LAM); Madre de Dios: *Foster & Wachter* 7336 (F,MO). **Bolivia**, Morillo: *Croat* 51417 (MO); Pando: *Nee* 31730 (NY). **Brazil**, Acre: *Steward* et al. P13209 (K); Mato Grosso: *Berg* et al. P19831 (K); Rondonia: *Prance* et al. 5253 (K).

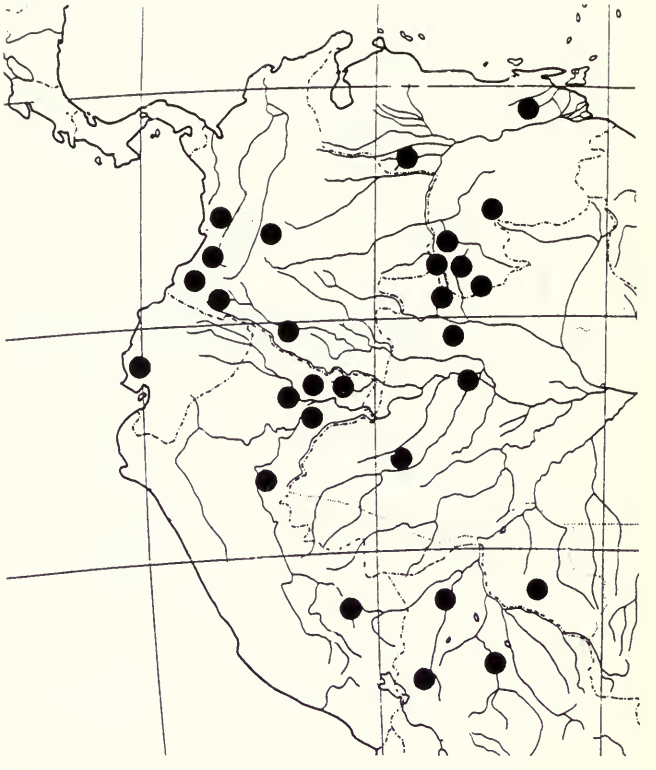

Fig. 45 Distribution of *P. coruscans*.

Piper coruscans can be distinguished by its distinctive ovate to suborbiculate leaves with steeply ascending, prominent secondary veins, and fruits that become suborbicular as they mature. Steyermark (1984) was responsible for reducing three species (*P. amazonicum*, *P. pseudochurumayu*, and *P. wurdackii*) into the synonymy of *P. coruscans*, explaining that the differences between them were not sufficient to maintain them as separate taxa. There are some slight differences in the shape of the leaf base, the degree of rugosity of the leaf surface, and the quantity of pellucid glands present, but these are within the range of variation for this species, and Steyermark's view is followed here.

52. **Piper scutilimbum** C. DC. in *Annu. Conserv. Jard. bot. Genève* **21**: 242 (1920). Type: Colombia, Santa Marta, *Smith* 1235 (G-holotype; BM!, MO!, NY!, S!-isotypes).
Fig. 46B, b, c.

Thin-stemmed shrub or small tree, 1.5–4 m high, stems glabrous. Leaves 16–27 (–31) cm long, 8–15 cm wide, oblong-elliptic, glandular, apex acuminate, base abruptly narrowed, cuneate or caudate, peltate. Venation with 6–10 pairs of secondary veins arising along the length of the midrib, arcuate-ascending, and 4–6 veins radiating around peltate base. Petioles sheathing, 2–5 cm long. Prophylls not apparent, if present hidden by sheathing petiole. Inflorescences 5–20 cm long, erect; peduncles 1.5–3.5 cm long. Anthers 0.2–0.3 mm long. Floral bracts 0.3–0.4 mm wide, triangular, ciliate. Fruits obovoid, 0.8–1.2 mm wide, trigonous, apex domed, glabrous or minutely granular; stigmas 3.

Tropical wet forest, cloud forest, and by sides of streams; 0–2000 m.

Fig. 46 A: *P. coruscans*, habit; a: bract and fruit. B: *P. scutilimbum*, habit; b: leaf with caudate base; c: bract and fruit.

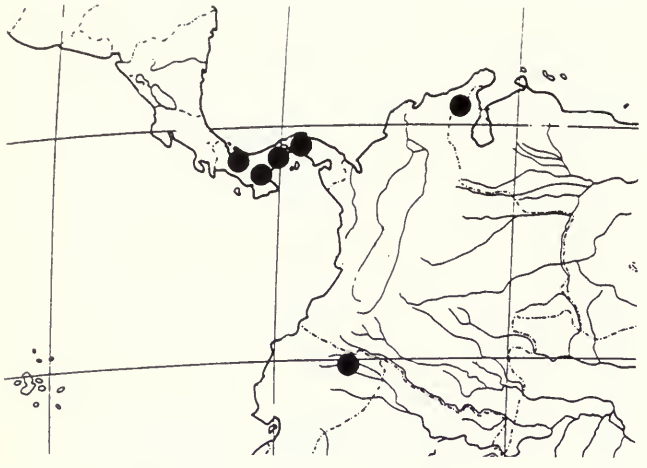

Fig. 47 Distribution of *P. scutilimbum*.

DISTRIBUTION. Panama–Ecuador. Fig. 47.

Panama, Bocas del Toro: *Kirkbride & Duke* 620 (MO); Chiriquí: *Hamilton & Stockwell* 3610 (MO); Colón: *Knapp* et al. 4464 (MO, BM); Veraguas: *Croat* 27424 (MO). **Ecuador**, Napo: *Cerron* 638 (MO); *Jipa* et al. DI959 (F).

This species has often been confused with *Piper veraguense* C. DC., because both species have peltate leaves. *P. scutilimbum* can be identified by its sheathing petioles and oblong-elliptic leaves narrowing abruptly towards the peltate bases. Some of the specimens from Ecuador (e.g. *Cerron* 638) have caudate leaf bases 1–2 cm long and about 0.5 cm wide. *P. veraguense* has ovate-lanceolate, peltate leaves without sheathing petioles. The bracts of *P. veraguense* are 0.6–1 mm wide, triangular-rhomboid and often cover the fruits in early stages, while those of *P. scutilimbum* are minute, 0.3–0.4 mm wide, and do not cover the fruits at any stage of development.

53. **Piper auritum** Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 54 (1816). Type: Crescit in regni Novae Hispaniae temperatis, *Humboldt* s.n. (P-holotype).
Fig. 48.

Schilleria aurita (Kunth) Kunth in *Linnaea* **13**: 713 (1839).
Artanthe aurita (Kunth) Miq., *Syst. piperac.*: 400 (1844).
A. seemanniana Miq. in Seemann, *Bot. voy. Herald*: 199, t.39 (1854). Type: Panama, southern Darien, *Seemann* 1069 (BM!-holotype).
Piper perlongipes Trel. in *Contr. U.S. natn. Herb.* **26**: 154 (1929). Type: Costa Rica, Pejivalle, Cartago, *Standley & Valerio* 46834 (US-holotype, photograph!).
P. alstoni Trel. in *Ann. Mo. bot. Gdn* **27**: 287 (1940). Type: Panama, El Valle, Coclé, *Alston & Allen* 1842 (ILL-holotype; MO!-isotype).
P. auritilimbum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **9**: 277 (1940). Type: Honduras, La Ceiba, Atlantida, *Yuncker, Koepper & Wagner* 8763 (ILL-holotype; K!, MO!, NY!-isotypes).
P. auritilaminum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **9**: 277 (1940). Type: Honduras, La Ceiba, Atlantida, *Yuncker, Koepper & Wagner* 8263 (ILL-holotype; NY!-isotype).
P. heraldi var. *cocleanum* Trel. in *Ann. Mo. bot. Gdn* **27**: 292 (1940). Type: Panama, vicinity of El Valle, Coclé, *Allen* 1192 (ILL-holotype; MO!-isotype).

Shrub or small tree, 1–6 m high, stems glabrous. Leaves 18–50 (–55) cm long, (11–)14–30 cm wide, oblong-elliptic, ciliate, upper surface with soft scattered hairs, undersurface with short hairs on veins, apex acute to obtuse, basal lobes deeply cordate, with one lobe considerably lower than other, not overlapping petiole. Venation with 4–6 pairs of secondary veins mostly arising from the lower part of the midrib. Petioles sheathing, 4–9 (–10) cm long, glabrous or with minute hairs. Prophylls not apparent, if present hidden by sheathing petiole. Inflorescences 15–30 (–37) cm long, erect, often arching, white or cream; peduncles 4–11 cm long, glabrous. Anthers 0.2–0.4 mm long. Floral bracts 0.5–0.8 mm wide, orbicular or triangular, white-ciliate. Fruits 0.6–0.8 mm wide, obovoid, trigonous, glabrous; stigmas 3.

Moist soil in disturbed areas such as tracks and roadsides, forest clearings, stream banks, landslides and edges of pasture; 0–1200 (–2000) m.

DISTRIBUTION. Mexico–Colombia, West Indies. Fig. 49.

Mexico, Chiapas: *Matuda* 4743 (NY); Quintana Roo: *Tellez* 3074 (BM); San Luis Potosi: *Pringle* 3693 (MU); Tabasco: *Cowan* 2334 (NY); Veracruz: *Gentry & Lott* 32620 (BM, MO); Yucatan: *Gaumer* 23276 (MO). **Belize**, Cayo: *Dwyer* 12715 (MO); Corozal: *Gentle* 442 (LA); Stann Creek: *Gentry* 8004 (MO); Toledo: *Whitefoord* 1662 (BM). **Guatemala**, Alta Verapaz: *King* 3314 (NY); Izabal: *Jones & Facey* 3219 (NY); Petén: *Ortiz* 412 (NY); San Marcos: *Croat* 40796 (MO); Retalhuleu: *Cosminsky* 114 (F). **Honduras**, Atlantida: *Webster & Miller* 12685 (MO); Colon: *Hagen* 1363 (NY); Comayagua: *Yuncker, Dawson & Youse* 6224 (MO); Cortés: *Blackmore & Chorley* 4004 (BM); Morazan: *Trochez* 45 (NY); Olancho: *Blackmore & Heath* 1769 (BM); Yoro: *MacDougal* et al. 3216 (BM,MO). **El Salvador**, Sonsonate: *Standley* 19328 (NY). **Nicaragua**, Bluefields: *Proctor* et al. 27282 (NY); Chinandega: *Baker* 85 (NY); Chontales: *Pipoly* 1589 (CAS); Granada: *Guzman* et al. 1705 (BM); Jinotega: *Grijalva & Araquistain* 229 (BM); Matagalpa: *Stevens* 11991 (M); Rio San Juan: *Araquistain* 3208 (BM); Zelaya: *Araquistain* 3035 (BM). **Costa Rica**, Alajuela: *Webster & Miller* 12210 (MO); Cartago: *Croat* 567 (MO); Heredia: *Bawa* 613 (MO); Limón: *Davidson* 6867 (LA); Puntarenas: *Raven* 22032 (DS); San José: *Tonduz* 2386 (CM). **Panama**, Bocas del Toro: *Blum* 1341 (MO); Canal Zone: *Croat* 5231 (NY); Chiriquí: *Liesner* 5 (MO); Coclé: *Correa* 55 (MO); Colón: *Nee* 7273 (MO); Darien: *Garwood* et al. 172 (BM); Panama: *Carrasquilla* et al. 224 (MO); San Blas: *Sugden* 535 (MO); Veraguas: *Folsom & Edwards* 3403 (BM). **West Indies**, Jamaica: *Houston* s.n. (BM). **Colombia**, Antioquia: *Scolnik* et al. 19An332 (BM); Chocó: *Killip & Garcia* 33550 (BM); El Valle: *Pennell* et al. 8578 (K, NY, US); Santander: *Haught* 1806 (BM).

Piper auritum is one of the most common New World species of *Piper*, growing at the edges of woods or in clearings and open sites. Its distinctive large, deeply-lobed leaves with sheathing petioles, and pale arching inflorescences make it easy to recognize. When crushed, the stems and leaves emit a strong smell of aniseed. Sterile specimens have sometimes been confused with species such as *P. obliquum* of section *Macrostachys*, which also has sheathing petioles. However, the inflorescence of *P. auritum* is slender and erect rather than substantial and pendulous as in *P. obliquum*, and the

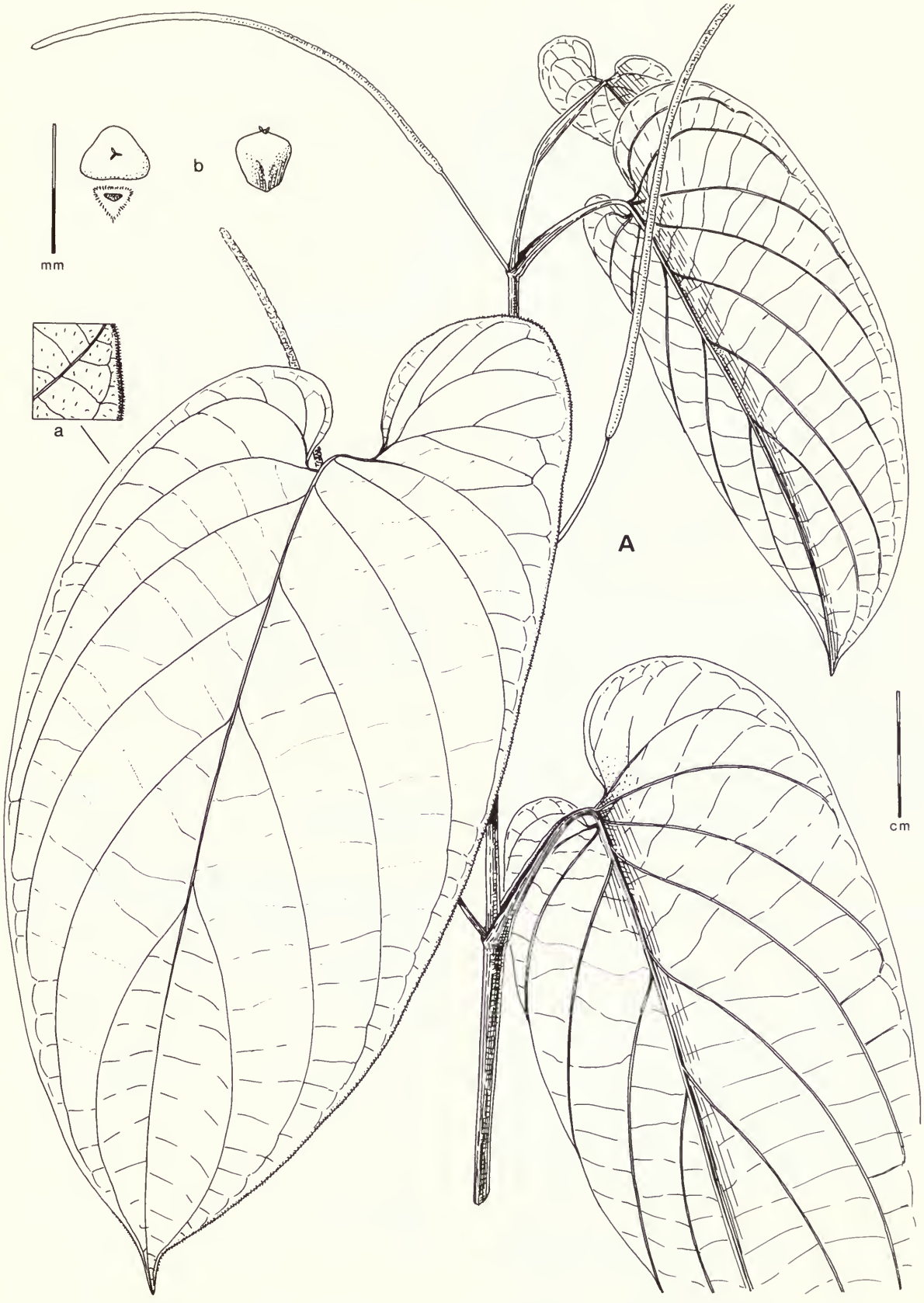

Fig. 48 *P. auritum* A: habit; a: part of leaf showing pubescent margin; b: bract and fruit.

Fig. 49 Distribution of *P. auritum*.

fruits are small and trigonous. The leaves of *P. auritum* have a distinct margin of short white hairs, a character that is shared with *P. marginatum* of section *Radula*. *Piper auritum* also has other characters in common with this species, such as sheathing petioles and arching, white or cream inflorescences. The fruits of *P. marginatum*, dark in colour and round from above with a raised rim, are considerably different from those found in section *Churumayu*. Arching inflorescences are also found elsewhere in section *Radula*, e.g. *P. aduncum* L. The vigorous climber, *P. multiplinervium* C. DC., also in section *Radula*, has sheathing petioles and similar fruits to those of *P. marginatum*. *P. auritum* displays characters linking sections *Churumayu* and *Radula*.

Excluded species

Piper abutiloides (Kunth) C. DC. in DC., *Prodr.* **16** (1):329 (1869).

This species compares well vegetatively with *P. regnellii* (Miq.) C. DC. However, Kunth's original description of *P. abutiloides* (as *Schilleria abutiloides*) emphasized that the fruits were not available ('haud suppetunt'). The only specimen seen for this study (not the type), identified as *P. abutiloides*, has an immature inflorescence. Without the presence of mature inflorescences, it is impossible to make a definite statement regarding the combination of *P. abutiloides* and *P. regnellii*, especially as *P. abutiloides* would take precedence as the earliest published name.

ACKNOWLEDGEMENTS. My grateful thanks are due to Mr A. O. Chater, Dr C. Jarvis, and Mr J. R. Press of the Department of Botany, The Natural History Museum, and Dr A. J. Bornstein, Assistant Professor of Biology, Southeast Missouri State University, for advice and helpful comments. I would also like to thank the following herbaria for the loan of their specimens–B, C, CAS, E, F, ILL, K, MO, MU, S, and US.

REFERENCES

Burger, W. C. 1971. Piperaceae. *Flora costaricensis. Fieldiana Bot.* **35**: 5–227.
—— 1972. Evolutionary trends in the Central American species of *Piper* (Piperaceae). *Brittonia* **24**(4): 356–362.
Candolle, C. de. 1869. Piperaceae. *In* A.P. de Candolle, *Prodromus systematis naturalis regni vegetabilis* **16**(1): 235–471.
—— 1902. Piperaceae. *In* I. Urban, *Symbolae antillanae* **3**: 161–274.
Dietrich, A. 1831. *Species plantarum* **1**: 173.
Gomez Pompa, A. 1966. *Estudios botanicas en la region de Misantla, Veracruz*: 140–152. Mexico City.
Miquel, F. A. 1844. *Systema piperacearum*. Rotterdam.
Steyermark, J. A. 1984. *Flora de Venezuela*. Fundacion para la Educacion Ambiental.
Tebbs, M. C. 1989*a*. Revision of *Piper* (Piperaceae) in the New World 1. Review of characters and taxonomy of *Piper* section *Macrostachys*. *Bull. Br. Mus. nat. Hist.* (Bot.) **19**: 117–158.
—— 1989*b*. The climbing species of New World *Piper* (Piperaceae). *Willdenowia* **19**: 175–189.
Trelease, W. 1927. Piperaceae of Panama. *Contr. U.S. natn. Herb.* **26**(2): 15–50.
—— 1929. Piperaceae of Costa Rica. *Contr. U.S. natn. Herb.* **26**(4): 115–226.
Trelease, W. & Yuncker, T. G. 1950. *Piperaceae of northern South America* **1**: 1–434. Urbana.
Yuncker, T. G. 1972. Piperaceae of Brazil. *Piper* — Groups 1–4. *Hoehnea* **2**: 23–366.
—— 1973. Piperaceae of Brazil. *Piper* — Group 5. *Hoehnea* **3**: 29–284.

INDEX

Accepted names are in roman and synonyms in *italic*, new names and principal references are in **bold**. An asterisk (*) denotes a figure.

Artanthe 194
Artanthe adenophylla Miq. 200
A. amazonica Miq. 232
A. aurita (Kunth) Miq. 234
A. benthamiana Miq. 213
A. brachypoda Benth. 227
A. colubrina (Link) Miq. 200
A. colubrina var. *crassifolia* Miq. 200
A. concinna Miq. 204
A. coruscans (Kunth) Miq. 232
A. denudans Miq. 209
A. glabella Miq. 200
A. grandifolia (Kunth) Miq. 209
A. jussiaeana (Kunth) Miq. 209
A. leptura (Kunth) Miq. 209
A. meyeniana Klotzsch ex Miq. 209
A. mikaniana (Kunth) Miq. 206
A. obovata (Kunth) Miq. 200
A. pseudochurumayu (Kunth) Miq. 232
A. regnellii Miq. 219
A. riparia (Kunth) Miq. 209
A. seemanniana Miq. 234
A. septuplinervia Miq. 231
A. subaequalis C. Presl 200
A. tejucensis Miq. 200
A. xylosteoides (Kunth) Miq. 203

section Callianira 223, 225
Carpunya lessertiana (Miq.) Presl 208
C. peruviana C. Presl 208
section Churumayu 194, 195, 236

Lindera benzoin Meissner 229

section Macrostachys 194, 195, 234

Ottonia carpunya (Ruiz López & Pavón) Miq. 208
O. lessertiana Miq. 208

Peltobryon attenuatum Klotzsch ex Miq. 200
Peperomia 200
P. obversa (M. Vahl) A. Dietr. 200
P. obovata (M. Vahl) A. Dietr. 200

Piper abutiloides (Kunth) C. DC. 236
Piper acutissimum Trel. 197
P. acutissimum var. *trichopus* (Trel.) Yuncker 197
P. aequale M. Vahl 194, 195, 196, 210*, **211**, 212, 212*, 213, 217, 225
P. aequale var. *elliptico-lanceolatum* C. DC. 211
P. albert-smithii Trel. & Yuncker 221
P. alstoni Trel. 234
P. altevaginans Trel. 197
P. amazonicum (Miq.) C. DC. 232
P. apiculatum C. DC. 200
P. arboreum Aublet 195, 197
P. arieianum C. DC. 197
P. arundinetorum Trel. 225
P. atrichopus Trel. 211
P. atrichopus var. *arborescens* Trel. 215
P. atroglandulosom Tebbs 194, 195, 196, 197, 199, **200**, 201*, 202, 202*
P. auritilaminum Trel. 234
P. auritilimbum Trel. 234
P. auritum Kunth 194, 195, 196, **234**, 235*, 236*
P. baryanum C. DC. 232
P. belemense C. DC. 200
P. benthamianum (Miq.) C. DC. 213
P. borucanum C. DC. 209
P. brachypodon (Benth) C. DC. 194, 195, 196, 225, 226*, **227**, 229, 229*
P. bryogetum C. DC. 229
P. cabagranum C. DC. 211
P. cadenaensis Tebbs 194, 196, **218**, 218*, 219*
P. caeruleifolium Trel. 211
P. caripense Kunth 211
P. carpunya Ruiz Lopéz & Pavón 195, 196, 207*, **208**, 208*, 231
P. carnosicaule Trel. 212
P. carrilloanum C. DC. 215, 217
P. casimirianum Hemsley 215, 217
P. cercidiphyllum Trel. 209
P. cheyennense Trel. & Standley 211
P. chiriquinum C. DC. 211
P. churumayu Poeppig 195
P. cocherense Trel. 208
P. colemanense Trel. 211
P. collinum var. *flagellicuspe* Trel. 215
P. colubrinum Link 200
P. concepcionis Trel. 225, 227
P. concinnatoris Yuncker 204
P. concinnifolium Trel. 211
P. concinnum (Miq.) C. DC. 204
P. corrugatum Kuntze 195, 196, **213**, 214*, 215*, 217, 221
P. coruscans Kunth 194, 195, 196, **232**, 232*, 233*
P. coruscans var. *membranaceum* (C. DC.) Steyerm. 232
P. costaricense C. DC. 211
P. crassifolium (Miq.) C. DC. 200
P. crassum Vell. Conc. 200
P. crispans Trel. ex Standley 211
P. debile C. DC. 206
P. debilicaule Trel. & Yuncker 227
P. densispicatum Steudel 200
P. denudans (Miq.) C. DC. 209
P. denudans var. *angustifolium* C. DC. 209
P. dilatatum C. DC. 195
P. divaricatum Meyer 196, **200**, 201*, 203*
P. dolichotrichum Yuncker 194, 195, 196, 223, **225**, 225*, 226*, 227, 229
P. donnell-smithii C. DC. ex J.D. Smith 211
P. dumosum Rudge 196, 201*, **202**, 203*
P. dupasquieri C. DC. 209
P. epilosipes Trel. 211
P. epunctulatum C. DC. 219
P. exigens Trel. 215
P. exigens var. *subovatum* Trel. 215
P. flabellinerve C. DC. 219
P. flavirameum C. DC. 225
P. flavirameum var. *obscurum* Trel. 227
P. fortunaensis Tebbs 194, 196, **223**, 224*, 225, 225*
P. frioense Standley & Steyerm. 211
P. fulvescens C. DC. 219
P. fulvescens var. *geraense* C. DC. 219
P. fulvescens var. *subglabrum* C. DC. 219
P. fuscum C. DC. 209
P. generalense Trel. 197
P. glabellum (Miq.) C. DC. 200
P. glabrilimbum C. DC. 200
P. glanduligerum C. DC. 213
P. gorgonae-insulae Trel. & Yuncker 197
P. glaziovii C. DC. 209
P. grande M. Vahl 194, 195, 196, 207*, **208**, 209, 209*
P. grandifolium Kunth 208
P. grandilimbum C. DC. 221
P. guanacostense C. DC. 194, 195, **197**, 197*, 198*
P. guedesii C. DC. 202
P. heraldi var. *cocleanum* Trel. 234
P. heterophyllum Ruiz Lopez & Pavón 200
P. imberbe Trel. & Standley 196, **202**, 204*, 207*
P. impunctatum Link 200
P. insipiens Trel. & Yuncker 202
P. jericoense Trel. & Yuncker 211
P. johnstoni C. DC. 211
P. jussiaeanum Kunth 209
P. lanceifolium Kunth 195
P. ledezmae Trel. & Yuncker 231
P. leiophyllum C. DC. 200
P. lenticellosum C. DC. 208
P. lepturum (Kunth) C. DC. 196, **209**, 210*, 211, 211*
P. lepturum var. *angustifolium* (C. DC.) Yuncker 209
P. lessertianum (Miq.) C. DC. 208
P. levilimbum Trel. 215
P. marginatibaccum Trel. ex Standley 197
P. marginatum Jacq. 195, 236
P. marmoreum Trel. 209
P. matinanum C. DC. 229
P. megalophyllum C. DC. 215, 217
P. megalophyllum var. *connivens* C. DC. 215
P. micranthera C. DC. 211
P. middlesexense Trel. 215, 217
P. mikanianum (Kunth) Steudel 194, 196, 204, 205*, **206**, 208
P. mikanianum f. *clausum* Yuncker 206
P. mikanianum var. *peltatum* Yuncker 206
P. misionesanum C. DC. 206
P. multiplinervium C. DC. 236

P. mutisii Trel. & Yuncker 221
P. nemorense C. DC. 213
P. nitidum M. Vahl 200, 202
P. novo-granatense C. DC. 231
P. nudicaule C. DC. 212
P. obliquum Ruiz López & Pavón 234
P. oblongilimbum C. DC. 202
P. obovatum M. Vahl 200
P. obovatum Ruiz López & Pavón 194, 200
P. obversum M. Vahl 200
P. omega Trel. 215
P. opacibracteum Trel. 229
P. oppressum Trel. 211
P. orenocanum C. DC. 232
P. ottoniifolium C. DC. 194, 195, 196, **229**, 229*, 230*
P. ottoniifolium var. *frutescens* Trel. & Yuncker 194, 231
P. ottoniifolium var. *latifolium* Trel. & Yuncker 194, 231
P. pablense Trel. 211
P. pabstii C. DC. 204
P. pallescens C. DC. 219
P. partiticuspe Trel. 213
P. parthenium C. DC. 206
P. parthenium var. *pilosius* C. DC. 206
P. paso-anchoense Trel. 211
P. paulownifolium C. DC. 215
P. peltaphyllum C. DC. 221
P. pendens Trel. 227
P. pendens var. *infaustum* Trel. 227
P. perbrevicaule Yuncker 195, 196, 221*, 222*, **223**
P. perbrevicaule var. *subglabrilimbum* Yuncker 223
P. pergamentifolium Trel. & Standley 215
P. perlasense Yuncker 211
P. perlongipes Trel. 234
P. portachueloense Trel. & Yuncker 197
P. pseudochurumayu (Kunth) C. DC. 232
P. pseudochurumayu var. *membranaceum* C. DC. 232
P. pseudo-variabile Trel. 209
P. pseudo-variabile var. *collium* Trel. 209
P. pseudo-variabile var. *pachypus* Trel. 209
P. regnellii (Miq.) C. DC. 194, 195, 196, **219**, 219*, 220*, 221, 236
P. regnellii var. *glabrius* C. DC. 219
P. regnellii var. *pallescens* (C. DC.) Yuncker 219
P. regnellii var. *parvifolium* C. DC. 219
P. reptabundum C. DC. 195, 196, 222*, **223**, 223*, 225
P. riitoense Trel. & Yuncker 197
P. riparense C. DC. 213
P. riparium Kunth 208
P. rubripes Trel. ex Standley 211
P. rupununianum Trel. & Yuncker 196, 198*, **199**, 200, 200*
P. saltuum C. DC. 197
P. sarapiquinum C. DC. 204
P. schiedeanum Steudel 194, 195, 196, 212, **213**, 216*, 217, 217*, 219, 221
P. schlimii C. DC. 197
P. scleromyelum C. DC. 231
P. scutilimbum C. DC. 194, 195, 196, 221, **232**, 233*, 234*
P. seducentifolium Trel. 197
P. seductum Trel. 211
P. septuplinervium (Miq.) C. DC. 194, 196, 230*, **231**, 231*
P. septuplinervium var. *subpubinervium* Yuncker 231
P. sievekingii C. DC. 209
P. spissinervium Trel. 209
P. subaequale (C. Presl) C. DC. 200
P. subdurum Trel. ex Standley 208
P. subrepens Trel. 194, 197, **204**, 205*, 206, 206*
P. subsessilifolium C. DC. 194, 195, 196, **225**, 227, 227*, 228*, 229
P. subvariabile Trel. 209
P. sulcinervosum Trel. 227
P. tejucense (Miq.) C. DC. 200
P. tenuifolium C. DC. 213
P. tenuispicum C. DC. 211
P. tiliifolia Schldl. & Cham. 213
P. trichopus Trel. 197
P. trigonum C. DC. 195, 196, **197**, 198*, 199, 199*
P. tsakianum C. DC. 213
P. urophyllum C. DC. 195, 196, **204**, 205*, 206, 206*, 208
P. urostachyum Hemsley 223, 225
P. vallicolum C. DC. 215
P. variabile C. DC. ex J. D. Smith 215, 217
P. variabile var. *obtentum* Trel. 215
P. veraguense C. DC. 194, 195, 196, 209, 213, 217, 220*, **221**, 221*, 234
P. veraguense var. *mutisii* (Trel. & Yuncker) Steyerm. 221
P. veraguense var. *venezuelense* Steyerm. 221
P. verruculosum C. DC. 194, 195, 196, 210*, **212**, 213, 213*
P. wurdackii Yuncker 232
P. xanthostachyum C. DC. 194, 195, 196, **227**, 228*, 229, 229*
P. xylosteoides (Kunth) Steudel 197, **203**, 204, 204*, 205
P. zacuapanum C. DC. 215, 217
P. zarceroense Trel. ex Standley 215
P. zingiberinum Trel. ex Standley 212

section Radula 195, 236

Schilleria abutiloides Kunth 236
S. aurita (Kunth) Kunth 234
S. colubrina Link ex Kunth 200
S. coruscans (Kunth) Kunth 232
S. grandifolia (Kunth) Kunth 209
S. jussiaeana Kunth 209
S. leptura Kunth 209
S. mikaniana Kunth 206
S. obovata Kunth 200
S. riparia (Kunth) Kunth 209
S. xylosteoides Kunth 203

Steffensia pseudochurumayu Kunth 232

OBITUARY

Ivan Mackenzie Lamb 1911–1990

Ivan Mackenzie Lamb was born in London on 10 September 1911 and died in Massachusetts, U.S.A., on 28 January 1990 after a long illness. He was educated at the University of Edinburgh, where he obtained a Ph.D. for research in mycology. In the mid-1930s three additional posts of Assistant Keeper were created in the Department of Botany at the British Museum (Natural History), London. Lamb was appointed on 14 January 1935 to the first of these, which was for work on lichens. The other two of these posts were for work on flowering plants, filled later in the same year by W. R. Philipson, and on diatoms, filled by myself in October 1936. I was, in consequence, a colleague of Lamb's from then until mid-1940 when I was transferred to other work for the duration of the war. I cannot say, though, that I came to know him well. He was a quiet and reserved person, always perfectly amiable and polite and never difficult to deal with, but not inclined to chat. Although never abrupt or dismissive, he was obviously anxious to get back to his work as soon as the matter that had caused one to interrupt him had been dealt with. In this he was a great contrast to his nearest neighbour in the Cryptogamic Herbarium, Geoffrey Tandy.

Lamb was a conscientious objector and continued to work in the museum until 20 September 1943. During this period he completed a monograph on *Neuropogon*, especially its Antarctic species, and followed this by work on *Placopsis*, another genus with many Antarctic representatives. This brought him in touch with J. W. S. Marr, a biologist with Discovery Investigations, who became commander of Operation Tabarin, an expedition to the Antarctic mounted to safeguard British interests in that area. Marr recruited Lamb as the botanist on this expedition and he spent two years in the Antarctic, one at Port Lockroy and one at Hope Bay. It is clear from the obituaries in *The Daily Telegraph* (20 February 1990) and *The Independent* (5 March 1990), both obviously written by other members of the expedition, that Lamb earned the respect and affection of his companions not only for his personality but also for his physical toughness. For his service on this expedition, Lamb was awarded the Polar Medal in silver with Antarctic clasp.

Only about a year after his return to the museum, Lamb resigned in 1946 and accepted the post of Professor of Cryptogamic Botany at Tucumán University in Argentina in 1947. He had by then married and his wife suffered badly from arthritis. He thought that the change in climate would help to alleviate this. In 1950, however, he moved to the Canadian National Museum, Ottawa, as curator of cryptogams. This, too, was a post that he held for only three years, for in 1953 he became Director of the Farlow Herbarium of Harvard University at Cambridge, Mass., U.S.A., a position he held until he left in 1972. Afterwards he changed his name to Elke Mackenzie. During these years he continued his work and varied correspondence on lichens and published his monumental *Index Nominum Lichenum* (1963), Antarctic lichens (1964, 1968), and monographs of *Leprocaulon* (1974, with A. Ward) and *Stereocaulon* (1977, 1978). Soon after his retirement he also did some work on marine algae of the New England coast, and published short papers on these. All Lamb's publications have a very high reputation. He will be long remembered for his dedicated, if isolated, research on Antarctic matters.

R. Ross

British Museum (Natural History) Publications

FLORA MESOAMERICANA

Flora Mesoamericana, a joint project of the Instituto de Biología, Universidad Nacional Autónoma de México, Missouri Botanical Garden, St. Louis, and The Natural History Museum, London, will start in 1991 with the publication of Vol 6, covering half of the monocotyledonous families. The entire work will be in 7 volumes published in Spanish at approximately 2-yearly intervals. It will comprise a concise identification manual for the vascular plants of Mesoamerica. The work incorporates much new research and will form a data base for the floristics and taxonomy of the region.

A Preliminary Bibliography of the Mesoamerican Flora
R. J. Hampshire, D. A. Sutton

1988, 245 × 175mm, 194pp.
0 565 01068 9 Paperback **£15.00**

THE CORALLINE RED ALGAE
An analysis of the genera and subfamilies of the nongeniculate Corallinaceae

W. J. Woelkerling

Nongeniculate coralline red algae (Corallinales, Rhodophyta) are both abundant in and vital to coral reefs, cementing the coral animal skeletons into a durable reef framework. In colder waters they form pavements of many square kilometres on the sea bed. It is one of the aims of this study to help resolve outstanding difficulties relating to taxonomy of the group. Extremely well illustrated with over 60 pages of scanning electron micrographs.

1988, 245 × 176mm, 268pp, 82 scanning electron micrographs, 259 figs, 19 tables.
Co-published with Oxford U.P.
0 198 54249 6 Hardback **£40.00**

Taxonomy and Biogeography of Macquarie Islands Seaweeds
R. W. Ricker.
1987, 175 × 250mm, 344pp, 126 figs.
0 565 00998 2 Hardback **£40.00**

SEAWEEDS OF THE BRITISH ISLES

Vol. 1. Part 1. Rhodophyta. Introduction, Nemaliales, Gigartinales. *P. S. Dixon & L. M. Irvine.*
1977, xi + 252pp, 90 figs.
0 565 00781 5 Paperback **£15.00**

Vol. 1. Part 2A. Cryptonemiales (*sensu stricto*), Palmariales, Rhodymeniales. *L. M. Irvine.*
1983, xii + 115pp, 28 figs.
0 565 00871 4 Paperback **£15.00**

Vol. 3. Part 1. Fucophyceae (Phaeophyceae). *R. L. Fletcher.*
1987, 145 × 210mm, 359pp, 90 figs, 15 plates.
0 565 00992 3 Paperback **£30.00**

Vol. 4. Tribophyceae (Xanthophyceae). *T. Christensen.*
1987, 145 × 210mm, 36pp, 8 figs.
0 565 00980 X Paperback **£7.50**

Vol. 2. Chlorophyta. *E. M. Burrows.*
To be published in 1991. Details to be announced.

CONTENTS

153 **The marine algal flora of Namibia: its distribution and affinities**
George W. Lawson, Richard H. Simons & William Edwin Isaac

169 **The infragenic classification of *Gentiana* (Gentianaceae)**
Ting-Nung Ho & Shang-Wu Liu

193 **Revision of *Piper* (Piperaceae) in the New World**
2. The taxonomy of *Piper* section *Churumayu*
Margaret Cecilia Tebbs

Bulletin British Museum (Natural History)
BOTANY SERIES
Vol. 20, December 1990